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Carlos A. Gonzalez-Benecke [a,*], Salvador A. Gezan [a], Timothy J. Albaugh [b], H. Lee Allen [c], Harold E. Burkhart [b], Thomas R. Fox [b], Eric J. Jokela [a], Chris A. Maier [d], Timothy A. Martin [a], Rafael A. Rubilar [e], Lisa J. Samuelson [f]

[a] School of Forest Resources and Conservation, P.O. Box 110410, University of Florida, Gainesville, FL 32611, USA
[b] Department of Forest Resources and Environmental Conservation, 319 Cheatham Hall, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[c] Department of Forestry and Environmental Resources, P.O. Box 8008, North Carolina State University, Raleigh, NC 27695, USA
[d] USDA Forest Service, Southern Research Station, 3041 E Cornwallis Road, Research Triangle Park, NC 27709, USA
[e] Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile
[f] School of Forestry and Wildlife Sciences, 3301 SFWS Building, Auburn University, Auburn, AL 36849, USA

ABSTRACT

There is an increasing interest in estimating biomass for loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*), two of the most ecologically and commercially important tree species in North America. The majority of the available individual-tree allometric models are local, relying on stem diameter outside bark at breast height (dbh) and, in some cases, total tree height (H): only a few include stand age or other covariates. Using a large dataset collected from five forestry research institutions in the southeastern U.S., consisting of biomass measurements from 744 loblolly pine and 259 slash pine trees, we developed a set of individual-tree equations to predict total tree above-stump biomass, stem biomass outside bark, live branch biomass and live foliage biomass, as well as functions to determine stem bark fraction in order to calculate stem wood biomass inside bark and stem bark biomass from stem biomass outside bark determinations. Local and general models are presented for each tree attribute. Local models included dbh or dbh and H as predicting variables. General models included stand-level variables such as age, quadratic mean diameter, basal area and stand density. This paper reports the first set of local and general allometric equations reported for loblolly and slash pine trees. The models can be applied to trees growing over a large geographical area and across a wide range of ages and stand characteristics. These sets of equations provide a valuable alternative to available models and are intended as a tool to support present and future management decisions for the species, allowing for a variety of ecological, silvicultural and economic applications, as regional assessments of stand biomass or estimating ecosystem C balance.

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1. Introduction

The southern pines are among the most studied forest trees in the world, and have significant commercial and ecological value. In the southeastern United States there are approximately 83 million ha of timberland and more than 28 million ha of southern pine forests, from which 15 million ha corresponds to southern pine plantations (Wear and Greis, 2012). This forested area produces about 58% of the total U.S. timber harvest and about 18% of the global supply of industrial roundwood, making this region one of the most important timber production zones in the world (McKeand et al., 2003; Allen et al., 2005; Fox et al., 2007). In this region, 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, with 79% of the planted slash pine occurring in Florida and Georgia (Barnett and Sheffield, 2005). Loblolly pine (*Pinus taeda* L.) grows on a variety of site types from east Texas to southern Tennessee to north Florida to southern New Jersey, and is one of the fastest growing pine species, planted in more than 10 million ha in the southeastern U.S. (Wear and Greis, 2012; Huggett et al., 2013). Both species 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, 2005).

Estimates of individual tree and component biomass are of interest to researchers, managers and policymakers (Jenkins et al., 2003). Measures of above-ground biomass are needed for estimating site productivity, and stand and tree growth and yield (Madgwick and Satoo, 1975). In addition, crown biomass estimates, together with harvesting techniques, determine the amount of logging residues and fire load, are necessary for planning prescribed fire and accounting for biomass for bioenergy production (Johansen and McNab, 1977; Hepp and Brister, 1982; Peter, 2008). Soil scientists and ecologists are also interested in quantifying biomass removals due to harvests, as they are concerned with its effects on site productivity and nutrient depletion (Powers et al., 1996; Shan et al., 2001; Sanchez et al., 2006). Ecologists are also interested in accurate estimations of stand biomass to analyze the effects of age and management on forest productivity (Ryan et al., 2006; Tang et al., 2014). In terms of greenhouse emissions mitigation, the forests in the southeastern and south-central U.S. could potentially capture CO_2 equivalent to about 23% of regional emissions (Han et al., 2007). The productivity and ubiquity of loblolly and slash pine make them key components of the carbon (C) balance of the United States. Hence, accurate estimates of tree biomass are central to our ability to understand and predict forest C stocks and dynamics (Galik et al., 2009; Johnsen et al., 2013).

Often, local functions used to estimate tree biomass rely on the stem diameter over-bark at breast height (dbh) (Swindel et al., 1979; Gholz and Fisher, 1982; Van Lear et al., 1984; Naidu et al., 1998; Jokela and Martin, 2000; Jenkins et al., 2003), or dbh and total tree height (H) as explanatory variables (White and Pritchett, 1970; Taras and Clark, 1975; Lohrey, 1984; Van Lear et al., 1986; Baldwin, 1987; Pienaar et al., 1987, 1996). These models are widely used but limited to certain stand characteristics and geographical areas, particularly those from which the data originated. However, inclusion of additional stand variables in these models such as stand age, density and/or productivity may improve the relationships, resulting in general models that provide more accurate predictions (Brown, 1997; Schmitt and Grigal, 1981; Alemdag and Stiell, 1982; Baldwin, 1987; Pienaar et al., 1987, 1996; António et al., 2007; Gonzalez-Benecke et al., 2014a). In addition, general models allow for better predictions on interpolation and extrapolation, allowing for more robust biological interpretation of the relationships under study because they account for the interaction between stand conditions and tree allometry.

Few general models are available in the literature that predicts above-stump biomass for loblolly (Baldwin, 1987; Pienaar et al., 1996) and slash pine trees (Pienaar et al., 1987). Those models, developed to predict stem component biomass, include only age, in addition to dbh and H, as predictors. Geographically generalized models are predictive equations fitted from data combined from many regions rather than a single location, such as site-specific biomass equations, and are generally applicable over the complete range of the aggregate data sources (Schmitt and Grigal, 1981). Using this geographically generalized approach, the objective of this study was to develop a set of individual-tree-level equations to estimate above-stump dry mass for different tree components for loblolly and slash pine trees, including local and general models that can be applied to trees of both species growing over a large geographical area and across a wide range of ages and stand characteristics, allowing for a variety of ecological, silvicultural and economics applications, from regional assessments of net primary productivity, to estimations of C budgets for life cycle analysis. The set of equations presented in this study provide a consistent basis for evaluations of southern pine forest biomass, improving the confidence in multi-scale analysis of C exchange between the forest and atmosphere.

2. Materials and methods

2.1. Data description

The dataset used to estimate the parameters for individual-tree above-stump biomass equations for loblolly and slash pine trees consisted of a collection of several sources used previously to publish site-specific allometric functions (Garbett, 1977; Manis, 1977; Gholz and Fisher, 1982; Gibson et al., 1985; Colbert et al., 1990; Baldwin et al., 1997; Albaugh et al., 1998Albaugh et al., 2004 Jokela and Martin, 2000; Adegbidi et al., 2002; Rubilar et al., 2005; Samuelson et al., 2004, 2008; Roth et al., 2007; Gonzalez-Benecke et al., 2010; Maier et al., 2012). The observations available corresponded to the raw data used for model fitting and not to the published equation estimates, as was the approach followed by Jenkins et al. (2003). This multi-source dataset was based on collaboration among five forestry research institutions in the southeastern U.S. Table 1 shows a summary of the number of trees measured by each institution for each species.

The dataset consisted of 744 loblolly pine and 259 slash pine trees measured at 25 and 14 sites, respectively. The data were collected across the natural range of the species distribution (Fig. 1), including trees from 2 to 36 years old, with dbh and H ranging between 1 to 35.6 cm and 1.5 to 25.7 m, respectively (Table 2). The data were collected 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, rotations and developmental stage. The stand characteristics at the time of sampling were thought to integrate changes in allometry due to changes in silviculture, site quality and stand age. Details on site descriptions and sampling procedure can be found in each of the publications previously mentioned. In all cases, destructive sampling was carried out. Trees were selected to include the range of sizes encountered in each study. Fresh weight of all tree components was recorded *in situ*. Dry mass was computed after discounting moisture content determined on samples of all components after being oven-dried at 65–70 °C to a constant weight.

The dataset included tree-level attributes, including dbh (cm), H (m) and dry weight of each tree above-ground tree component: living foliage (FOLIAGE, kg); living branches (BRANCH, kg); stem outside bark (STEM, kg) and the whole-tree above-stump biomass (TASB, the sum of all components in kg). In a subset of the trees, STEM was partitioned into stem wood (WOOD, kg) and stem bark (BARK, kg) biomass, and a ratio between STEM and BARK (BFRAC) was determined. A comparison between species for the general relationships between dbh and above-stump biomass components is presented in Fig. 2.

The dataset included stand-level variables that characterized the plot where each selected tree was growing before being cut for biomass determination. The stand-level variables included were: basal area (BA, m^2 ha^{-1}), trees per hectare (N, ha^{-1}) and stand age (AGE, years). Using N and BA, quadratic mean diameter (Dq, cm) was calculated and the ratio of dbh to Dq (Dp, cm cm^{-1}) was determined for each sampled tree. The variable Dp reflects the relative level of dominance of each tree within the plot. As site index (SI, m) was available for less than 30% of the whole dataset, that attribute was not included in the analysis. Stand-level variables associated with the 34 loblolly pine trees provided by Virginia Polytechnic Institute and State University were not available. Those trees were kept in the dataset as they provided valuable information due to the wide range in tree size and age, and were only used for fitting models that did not use stand-level variables. Details of tree and stand characteristics of the dataset used are summarized in Table 2.

Table 1
Summary biomass measurement per institution and species.

Species	Institution	Reference	n	AGE (yrs.)	Stand Type	Sampling Season
Loblolly (n = 744)	Auburn University	Samuelson et al. (2004)	48	2–6	Planted	Winter
		Samuelson et al. (2008)	11	10	Planted	Winter
	North Carolina State University	Tew et al. (1986)	10	22	Planted	Winter
		Albaugh et al. (1998)	16	8	Planted	Winter
		Albaugh et al., 2004	48	9–13	Planted	Winter
		Unpublished[a]	62	18–24	Planted	Winter
		Rubilar et al. (2005)	12	17	Planted	Winter
	Virginia Polytechnic Institute and	Baldwin et al. (1997)	34	9–30	Planted	Fall
	State University University of Florida	Colbert et al. (1990)	33	4	Planted	Fall
		Jokela and Martin (2000)	40	13	Planted	Fall
		Adegbidi et al. (2002)	72	1–4	Planted	Fall
		Roth et al. (2007)	101	2–5	Planted	Winter
		Unpublished[b]	60	2	Planted	Winter
	U.S. Forest Service	Gibson et al. (1985)	10	25	Planted	n.a.
		Maier et al. (2012)	137	2–4	Planted	Winter
		Unpublished[c]	50	3–17	Planted	Winter
Slash (n = 259)	University of Florida	Manis (1977)	29	2–9	Planted	Winter
		Garbett (1977)	12	27–36	Natural	Spring
		Gholz and Fisher (1982)	32	2–34	Planted	Winter
		Colbert et al. (1990)	34	4	Planted	Fall
		Jokela and Martin (2000)	40	13	Planted	Fall
		Roth et al. (2007)	84	2–5	Planted	Winter
		Gonzalez-Benecke et al. (2010)	16	8–16	Planted	Fall
		Unpublished[b]	24	2	Planted	Winter
	U.S. Forest Service	Gibson et al. (1985)	12	25	Planted	n.a.

n: number of observations; AGE: range of age of measured trees (yrs.).

[a] North Carolina State University provided data from unpublished studies (30 trees from two fertilization studies at age 7 and 8 year; 8 trees form an irrigation and fertilization study at age 18 and 24 year; and 24 trees from three site preparation studies at age 22 and 24 year).

[b] University of Florida provided data from unpublished studies (60 loblolly and 24 slash pine trees from three planting density x culture studies at age 2 year).

[c] US Forest Service provided data from unpublished studies (10 trees from a 3-year old stand; 16 trees from a Cross Carbon Study with trees of 7 year old; and 24 trees of 17 year-old from the Long Term Site Productivity project).
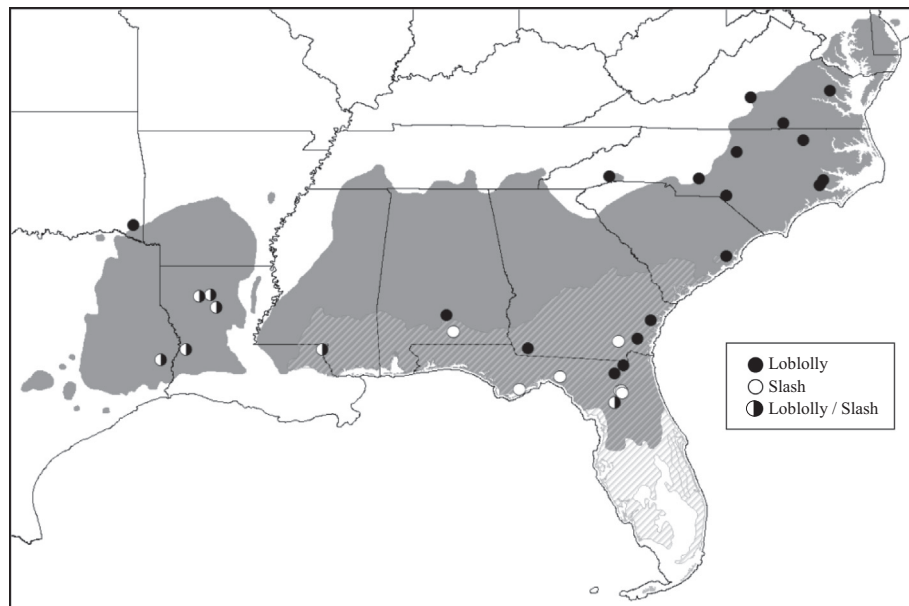
Fig. 1. Location of the study sites for loblolly pine (filled circles) and slash pine (open circles) within the species natural distribution range (loblolly = solid grey; slash = hashed). Sites where trees of both species were measured simultaneously are labeled with a filled and open circle.

Stem biomass including bark (STEM) was recorded for all trees. The separation of STEM into WOOD and BARK was carried out on a subset of 190 loblolly and 118 slash pine trees and BFRAC was determined for each of these trees. This data subset contained trees with AGE ranging between 3 and 30 years old for loblolly pine and 3 and 36 years old for slash pine, and dbh and H ranging between 1.0 and 35.4 cm and 1.6 and 22.4 m, respectively. The relationship between dbh and BFRAC for both species is shown in Fig. 3.

A summary of the stand level estimates of above-stump biomass (Mg ha^{-1}), woody biomass mean productivity (MAI$_W$, Mg ha^{-1} year^{-1}) and foliage biomass partitioning (pFT) is presented in Table 3. Data shown in Table 3 corresponds to the

Table 2
Summary statistics of individual-tree and their stand-level characteristics for measured loblolly and slash pine trees.

Species	Attribute	Unit	n	Mean	Std Dev	Minimum	Maximum
Loblolly	AGE	year	744	7.3	6.7	2	30
	dbh	cm	744	9.9	6.8	1.0	32.6
	H	m	744	7.6	5.1	1.8	25.7
	N	ha^{-1}	710	1425	525	420	2990
	BA	m^2 ha^{-1}	710	13.1	12.5	0.2	48.9
	Dq	cm	710	9.5	6.0	1.6	32.6
	Dp	cm cm^{-1}	710	1.0	0.3	0.2	2.8
	BRANCH	kg	744	6.4	10.5	0.1	117.0
	FOLIAGE	kg	744	3.5	3.2	0.0	25.9
	STEM	kg	744	30.1	57.3	0.2	450.2
	TASB	kg	744	39.9	69.5	0.6	593.0
	WOOD	kg	190	27.8	40.7	0.2	299.3
	BARK	kg	190	4.0	4.6	0.1	30.8
	BFRAC	kg kg^{-1}	190	0.17	0.05	0.08	0.36
Slash	AGE	year	259	10.2	10.7	2	36
	dbh	cm	259	9.9	7.3	1.3	32.6
	H	m	259	8.1	6.4	1.5	22.9
	N	ha^{-1}	259	1414	642	350	2990
	BA	m^2 ha^{-1}	259	12.0	11.9	0.3	43.6
	Dq	cm	259	10.0	7.1	2.1	25.8
	Dp	cm cm^{-1}	259	1.0	0.3	0.3	1.9
	BRANCH	kg	259	6.8	12.4	0.1	84.1
	FOLIAGE	kg	259	4.6	6.2	0.3	56.5
	STEM	kg	259	43.8	85.2	0.3	531.9
	TASB	kg	259	55.6	101.6	0.8	648.3
	WOOD	kg	118	45.3	62.1	0.2	467.5
	BARK	kg	118	9.0	9.5	0.2	64.4
	BFRAC	kg kg^{-1}	118	0.24	0.09	0.12	0.45

AGE: tree/stand age (yrs.); dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); N: trees per hectare (ha^{-1}); BA: stand basal area (m^2 ha^{-1}); Dq: quadratic mean diameter (cm); Dp:ratio between dbh and Dq (cm cm^{-1}); BRANCH: total living branch biomass (kg); FOLIAGE: total living needles biomass (kg); STEM: above-stump stem over bark biomass (kg); TASB: total above-stump biomass (kg); WOOD: above-stump stem wood inside bark biomass (kg); BARK: above-stump stem bark biomass (kg); BFRAC: ratio of BARK to STEM (kg kg^{-1}).
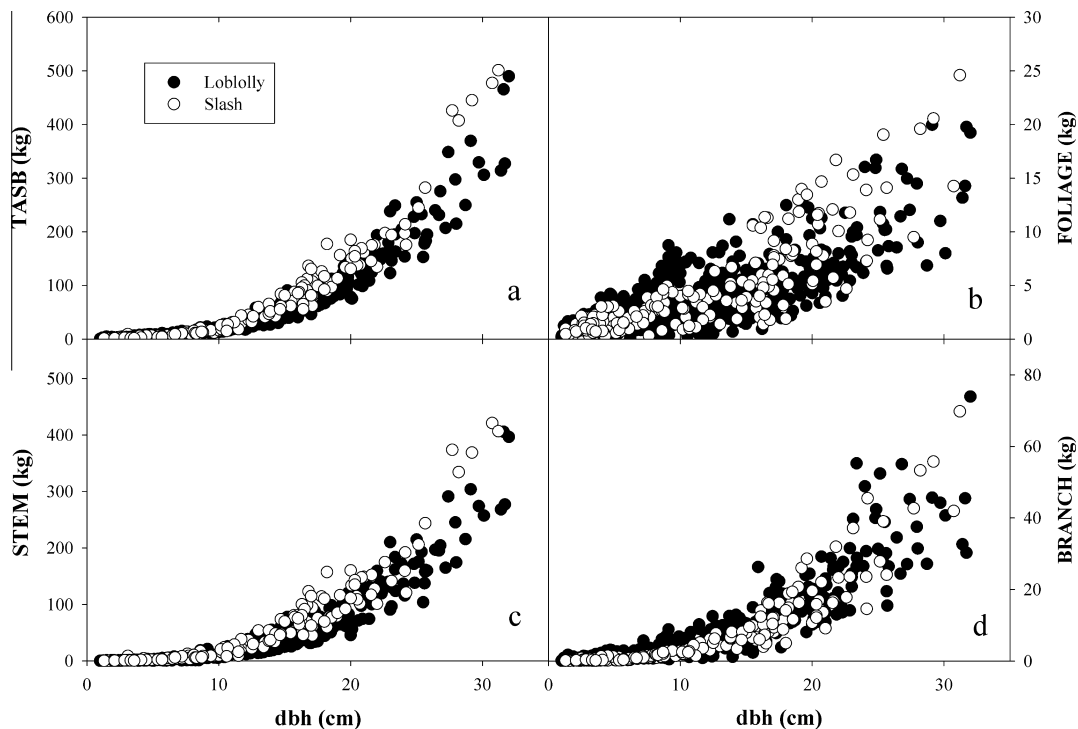
Fig. 2. Relationship between dbh and (a) total tree above-stump biomass (TASB, kg), (b) living foliage biomass (FOLIAGE, kg), (c) stem biomass outside bark (STEM, kg) and (d) branch biomass outside bark (BRANCH, kg) for loblolly (filled circle) and slash (open circle) pine trees growing in the southeastern U.S.

reported values for each study site where the raw data for model fitting was obtained (Fig. 1 and Table 1), and also includes other studies where stand-level biomass data were reported for both species. Stand-level above-stump biomass data were not available for Albaugh (unpublished); Baldwin et al. (1997), Garbett (1977), Gibson et al. (1985) and USFS (unpublished).

Fig. 3. Relationship between dbh and BARK to STEM fraction (BFRAC) for loblolly (filled circle) and slash (open circle) pine trees growing in the southeastern U.S.

2.2. Model description

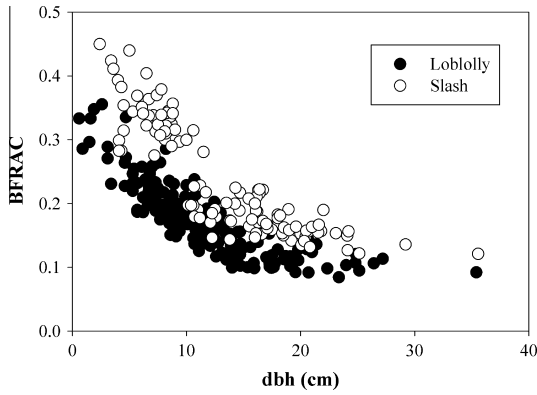We defined six sets of equations to estimate above-stump biomass that depend on data availability. In order to estimate WOOD and BARK, models were fitted to estimate BFRAC following the same procedure as for the above-stump biomass components. When BFRAC was known, BARK and WOOD were determined as: BARK = BFRAC·STEM and WOOD = (1−BFRAC)·STEM.

Set 1. When only dbh is known (for both species):

$$\text{TASB}, \text{STEM} = a_1 \cdot (\text{dbh}^{a_2}) + \varepsilon_i \tag{1}$$

$$\text{BRANCH}, \text{FOLIAGE} = a_1 \cdot (\text{dbh}^{a_2}) \cdot \exp(a_3 \cdot \text{dbh}) + \varepsilon_i \tag{2}$$

$$\text{BFRAC} = \exp(a_1 + a_2 \cdot \ln(\text{dbh})) + \varepsilon_i \tag{3}$$

where a_1, a_2 and a_3 are curve fit parameter estimates, exp is base of natural logarithm and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$. The model selected for FOLIAGE and BRANCH, proposed by Ruark et al. (1987), includes a second parameter estimate for the independent predictor and is called the variable allometric ratio model.

Set 2: when dbh and AGE are known (for both species):

$$\text{TASB}, \text{STEM} = b_1 \cdot (\text{dbh}^{b_2}) \cdot (\text{AGE}^{b_3}) + \varepsilon_i \tag{4}$$

$$\text{FOLIAGE}, \text{BRANCH} = b_1 \cdot (\text{dbh}^{b_2}) \cdot \exp(b_3 \cdot \text{dbh}) \cdot (\text{AGE}^{b_4}) + \varepsilon_i \tag{5}$$

$$\text{BFRAC} = \exp(b_1 + b_2 \cdot \ln(\text{dbh}) + b_3 \cdot \text{AGE}) + \varepsilon_i \tag{6}$$

where b_1 to b_4 are curve fit parameter estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$.

Set 3: when dbh, AGE and other stand parameters are known.

In addition to dbh and AGE, the inclusion of several stand-level variables as covariates in the above model was evaluated to improve the local biomass-dbh equation, which resulted in a general allometric equation. The variables considered as covariates, in addition to AGE, corresponded to N, BA, and Dp. These variables represented different aspects of the stand, such as stocking, productivity and competition, all of which could affect the biomass-diameter relationships. Similar to Crescente-Campo et al. (2010), to test which stand-level variables should be included in the final general model, a logarithmic transformation of the response variable was carried out and a stepwise procedure was used. A threshold significance value of 0.15 and 0.05 were used for variable selection criteria for a variable to enter and stay, respectively; and the variance inflation factor (VIF) was monitored to detect multicollinearity among explanatory variables. Variables included in the model with VIF larger than 5 were discarded, as suggested by Neter et al. (1996).

For loblolly pine, the models selected to estimate above-stump biomass using dbh, AGE and stand variables were:

$$\text{STEM} = c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{BA}^{c_3}) + \varepsilon_i \tag{7}$$

$$\text{TASB} = c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{N}^{c_3}) \cdot (\text{Dp}^{c_4}) + \varepsilon_i \tag{8}$$

$$\text{FOLIAGE} = c_1 \cdot (\text{dbh}^{c_2}) \cdot \exp(c_3 \cdot \text{dbh}) \cdot (\text{AGE}^{c_4}) \cdot (\text{N}^{c_5}) \cdot (\text{Dp}^{c_6}) + \varepsilon_i \tag{9}$$

$$\text{BRANCH} = c_1 \cdot (\text{dbh}^{c_2}) \cdot \exp(c_3 \cdot \text{dbh}) \cdot (\text{AGE}^{c_4}) \cdot (\text{N}^{c_5}) \cdot (\text{BA}^{c_6}) + \varepsilon_i \tag{10}$$

$$\text{BFRAC} = \exp(c_1 + c_2 \cdot \ln(\text{dbh}) + c_3 \cdot \ln(\text{Dq})) + \varepsilon_i \tag{11}$$

For slash pine, the models selected were:

$$\text{TASB} = c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{AGE}^{c_3}) \cdot (\text{Dp}^{c_4}) + \varepsilon_i \tag{12}$$

$$\text{STEM} = c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{AGE}^{c_3}) \cdot (\text{N}^{c_4}) + \varepsilon_i \tag{13}$$

$$\text{FOLIAGE} = c_1 \cdot (\text{dbh}^{c_2}) \cdot \exp(c_3 \cdot \text{dbh}) \cdot (\text{AGE}^{c_4}) \cdot (\text{N}^{c_5}) \cdot (\text{Dp}^{c_6}) + \varepsilon_i \tag{14}$$

$$\text{BRANCH} = c_1 \cdot (\text{dbh}^{c_2}) \cdot \exp(c_3 \cdot \text{dbh}) \cdot (\text{AGE}^{c_4}) \cdot (\text{Dp}^{c_5}) + \varepsilon_i \tag{15}$$

$$\text{BFRAC} = \exp(c_1 + c_2 \cdot \ln(\text{dbh}) + c_3 \cdot \text{AGE} + c_4 \cdot \ln(\text{N})) + \varepsilon_i \tag{16}$$

where c_1 to c_5 are curve fit parameters estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$.

Set 4: when dbh and H are known (both species):

$$\text{TASB}, \text{STEM} = d_1 \cdot (\text{dbh}^{d_2}) \cdot (H^{d_3}) + \varepsilon_i \tag{17}$$

$$\text{FOLIAGE}, \text{BRANCH} = d_1 \cdot (\text{dbh}^{d_2}) \cdot \exp(d_3 \cdot \text{dbh}) \cdot (H^{d_4}) + \varepsilon_i \tag{18}$$

$$\text{BFRAC} = \exp(d_1 + d_2 \cdot \ln(\text{dbh}^2 \cdot H)) + \varepsilon_i \tag{19}$$

where d_1 to d_4 are curve fit parameter estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$.

Set 5: when dbh, H and AGE are known.

For loblolly pine, the models selected to estimate above-stump biomass using dbh, H and AGE were:

$$\text{TASB}, \text{STEM} = e_1 \cdot (\text{dbh}^{e_2}) \cdot (H^{e_3}) \cdot (\text{AGE}^{e_4}) + \varepsilon_i \tag{20}$$

$$\text{FOLIAGE}, \text{BRANCH} = e_1 \cdot (\text{dbh}^{e_2}) \cdot \exp(e_3 \cdot \text{dbh}) \cdot (H^{e_4}) \cdot (\text{AGE}^{e_5}) + \varepsilon_i \tag{21}$$

$$\text{BFRAC} = \exp(e_1 + e_2 \cdot \ln(\text{dbh}^2 \cdot H) + e_3 \cdot \text{AGE}) + \varepsilon_i \tag{22}$$

For slash pine, the models selected were:

$$\text{TASB}, \text{STEM}, \text{FOLIAGE}, \text{BRANCH} = e_1 \cdot (\text{dbh}^{e_2}) \cdot (H^{e_3}) \cdot (\text{AGE}^{e_4}) + \varepsilon_i \tag{23}$$

$$\text{BFRAC} = \exp(e_1 + e_2 \cdot \ln(\text{dbh}^2 \cdot H) + e_3 \cdot \text{AGE}) + \varepsilon_i \tag{24}$$

where e_1 to e_5 are curve fit parameter estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$. Note that for slash pine, the second parameter estimate for dbh was not significant in the model to estimate FOLIAGE and BRANCH.

Set 6: when dbh, H, AGE and other stand attributes are known:

Following the same procedure of log-transformation of the response and variable selection criteria used for the biomass-dbh models, general models that include stand-level variables were also fitted for equations of set 5.

For loblolly pine, the models selected to estimate above-stump biomass using dbh, H, AGE and stand variables were:

$$\text{FOLIAGE} = f_1 \cdot (\text{dbh}^{f_2}) \cdot \exp(f_3 \cdot \text{dbh}) \cdot (H^{f_4}) \cdot (\text{AGE}^{f_5}) \cdot (\text{N}^{f_6}) \cdot (\text{Dp}^{f_7}) + \varepsilon_i \tag{25}$$

Table 3

Above-stump biomass (Mg ha^{-1}), woody biomass mean productivity (MAI$_W$, Mg ha^{-1} year^{-1}) and foliage biomass partitioning (FOLIAGE to TAGB ratio; pFT) for loblolly and slash pine stands.

Species	Reference	Age	Nha	FOLIAGE (Mg ha^{-1})	BRANCH (Mg ha^{-1})	STEM (Mg ha^{-1})	TAGB (Mg ha^{-1})	MAI$_W$ (Mg ha^{-1} year^{-1})	pFT
Loblolly	Adegbidi et al. (2002)[a]	2	1495	3.4	3.0	2.3	8.7	2.7	0.39
	Roth et al. (2007)[a]	2	1329–2990	2.6–5.8	1.8–3.6	2.2–6.7	6.6–16.1	0.61–0.64	0.36–0.39
	Samuelson et al. (2004)[a]	3	1040	3.5–6.4	2.5–4.7	3.4–5.7	9.4–16.8	2.0–3.5	0.37–0.38
	Adegbidi et al. (2002)[a]	4	1495	4.1	5.5	11.8	21.4	5.4	0.19
	Burkes et al. (2003)	4	740–3700	7.4–10.9	n.a.	9.3–28.9	n.a.	2.3–7.2	n.a.
	Colbert et al. (1990)[a]	4	1440–1453	0.8–9.1	0.4–10.1	0.8–15.8	1.9–32.2	0.3–6.5	0.28–0.42
	Maier et al. (2012)[a]	4	1280	4.2–5.9	3.8–5.9	11.7–17.5	19.7–29.3	4.7–6.2	0.20–0.21
	Roth et al. (2007)[a]	5	1227–2742	n.a.	n.a.	n.a.	23.5–65.3	n.a.	n.a.
	White and Pritchett (1970)	5	7175–8072	0.9–5.0	0.9–5.0	3.0–19.8	5.0–31.3	0.6–4.0	0.21–0.22
	Samuelson et al. (2004)[a]	6	920–960	4.8–9.4	8.2–15.2	24.2–47.7	37.2–72.3	5.4–10.5	0.13
	Albaugh et al. (1998)[a]	8	1260	1.8–3.6	2.2–3.1	4.4–6.6	8.4–13.3	1.0–1.7	0.21–0.27
	Samuelson et al. (2008)[a]	10	830–940	4.7–5.5	12–026	86–143	102.6–174.0	10.3–17.4	0.05–0.03
	Nemeth (1973)	11	1120–1400	4.9–5.9	7.8–9.4	54.7–65.6	65.0–78.0	4.9–5.9	0.08
	Kinerson et al. (1977)	12	1444	2.6	4.8	31.5	38.9	3.0	0.07
	Larsen et al. (1976)	13	740–3700	9.5	19.8	59	88.5	6.1	0.11
	Jokela and Martin (2000)[a]	13	1192–1538	3.9–10.5	8.0–29.3	33.1–116.1	45.0–155.2	3.2–11.2	0.07–0.09
	Will et al. (2006)	13	n.a.	3.5–7.6	11.3–17.2	72.2–170.4	87.0–195.2	6.4–14.4	0.04
	Hamilton et al. (2002)	15	1733	4.9–5.0	6.8–6.8	36.1–36.5	47.8–48.2	2.8–2.9	0.10–0.10
	Blazier (1999)	15	1292–1396	5.3–7.0	11.8–15.9	74.0–77.3	91.1–100.2	5.7–6.2	0.06 0.07
	Albaugh et al. (2004)[a]	16	1005–1255	2.2–5.4	4.0–9.7	29.9–80.6	44.7–107.4	2.8–6.7	0.05–0.05
	Jorgensen et al. (1975)	16	2243	8.0	23.2	124.8	156.0	9.2	0.05
	Kinerson et al. (1977)	16	1444	2.7	5.2	49.9	57.8	3.4	0.05
	Wells and Jorgensen (1975)	16	2200	8.0	14.6	124.8	147.4	8.7	0.05
	Johnson and Lindberg (1992)	17	1700	5.4	11.3	129.4	146.1	8.3	0.04
	Rubilar et al. (2005)[a]	18	1541	3.4	10.6	116.0	130.0	7.0	0.03
	Ku and Burton (1973)	19	n.a.	5.0–6.8	14.7–16.6	94.0–144.3	113.7–167.7	5.7–8.5	0.04
	Rolfe et al. (1977)	20	n.a.	6.9	27.3	117.1	151.3	7.2	0.05
	Rubilar et al. (2005)	22	695	5.1	19.9	118.2	143.2	6.3	0.04
	Tew et al. (1986)[a]	22	983	3.8	11.8	69.2	84.8	8.5	0.04
	Johnson and Lindberg (1992)	23	760	7.6	15.6	78.2	101.4	4.1	0.07
	Pehl et al. (1984)	25	1175	4.6	12.0	147.5	164.1	6.4	0.03
	Vogel et al. (2011)[b]	26	692–1346	7.0–11.4	16.0–25.6	64.0–119.6	87.0–156.6	3.1–5.6	0.07–0.08
	Johnson and Lindberg (1992)	35	430	3	15.4	98.8	117.2	3.3	0.03
	Van Lear et al. (1984)	41	437	2.5–3.2	12.6–17.7	83.4–111.5	98.5–132.4	2.3–3.2	0.02–0.03
	Van Lear and Kapeluck (1995) [c]	48	437	3.6	27.8	113.5	144.9	2.9	0.02
Slash	Manis (1977)[a]	1	850	0.03	0.01	0.02	0.05	0.02	0.60
	Gholz and Fisher (1982)[a]	2	1360–1424	0.08–0.10	0.01–0.02	0.04–0.06	0.15–0.19	0.07–0.09	0.53–0.57
	Roth et al. (2007)[a]	2	1324–2982	n.a.	n.a.	n.a.	3.8–8.8	n.a.	n.a.
	Manis (1977)[a]	3	1000	0.48	0.13	0.69	1.3	0.27	0.37
	Burkes et al. (2003)	4	740–3700	5.2–10.8	n.a.	7.4–25.7	n.a.	1.9–6.4	n.a.
	Colbert et al. (1990)[a]	4	1440–1453	1.5–5.6	0.5–3.2	2.3–15.3	4.3–23.6	0.7–9.7	0.24–0.36
	Gholz and Fisher (1982)[a]	5	1280–1648	1.0–2.0	0.23–0.57	2.6–4.9	4.0–7.5	0.6–1.1	0.25–0.27
	Manis (1977)[a]	5	1330	0.62	0.26	1.72	2.6	0.40	0.24
	Roth et al. (2007)[a]	5	1107–2608	n.a.	n.a.	n.a.	19.8–52.4	n.a.	n.a.
	White and Pritchett (1970)	5	5830–7623	2.8–11.7	1.8–6.2	12.0–43.7	16.7–61.6	2.4–8.7	0.17–0.19
	Gonzalez-Benecke et al. (2010)[a]	8	1904–2432	4.9–6.3	4.8–6.0	28.5–35.9	38.1–48.0	4.2–5.2	0.13
	Gholz and Fisher (1982)[a]	8	1712–1840	3.5–5.5	1.8–3.5	15.0–18.7	20.3–27.7	1.9–2.3	0.17–0.20
	Manis (1977)[a]	9	1050	2.2	2.2	12.5	16.9	1.6	0.13
	Jokela and Martin (2000)[a]	13	999–1423	5.7–13.2	8.2–23.9	48.7–106.2	62.7–142.8	4.8–11.0	0.09–0.09
	Gholz and Fisher (1982)[a]	14	976–1392	4.6–6.8	4.5–9.5	47.6–85.6	56.7 – 101.9	3.7–6.8	0.07 – 0.09
	Gonzalez-Benecke et al. (2010)[a]	16	1760–2096	9.8–10.8	11.8–13.4	65.1–72.3	85.9–95.3	4.8–5.4	0.11
	Shan et al. (2001)[d]	17	n.a.	4.2–6.8	5.7–10.2	75.6–125.6	85.5–142.6	4.8–8.0	0.05
	Gholz and Fisher (1982)[a]	18	976–1118	4.2–5.2	7.5–9.2	81.9–83.6	93.6–98.0	5.0–5.2	0.04–0.05
	Johnson and Lindberg (1992)	22	1056	4.8	7.4	94.1	106.3	4.6	0.05

Table 3 (continued)

Species	Reference	Age	Nha	FOLIAGE (Mg ha^{-1})	BRANCH (Mg ha^{-1})	STEM (Mg ha^{-1})	TAGB (Mg ha^{-1})	MAI$_W$ (Mg ha^{-1} year^{-1})	pFT
	Harding and Jokela (1994)	25	1181–1215	2.6–4.4	6.4–12.0	70.4–161.9	79.4–178.3	3.1–7.0	0.03–0.03
	Gholz and Fisher (1982)[a]	26	928–1280	4.8–6.6	9.1–18.6	100.1–148.8	114.9–172.1	4.2–6.3	0.04
	Vogel et al. (2011)[c]	26	538–1115	6.4–10.0	11.8–20.0	87.8–154.2	106.0–184.2	3.4–5.9	0.05–0.06
	Gholz and Fisher (1982)[a]	34	1280–1536	3.0–5.4	8.6–16.0	86.7–170.9	98.3–192.3	2.6–5.0	0.03
	Swindel et al. (1979)[d]	40	1066–1093	2.8–3.8	4.1–5.7	50.1–67.5	57.0–77.0	1.4–1.8	0.03–0.05

Nha: living trees per ha (ha^{-1}); FOLIAGE: total living needles biomass (Mg ha^{-1}); BRANCH: total living branch biomass (Mg ha^{-1}); STEM: above stump stem over bark biomass (Mg ha^{-1}); TASB: total above-stump biomass (Mg ha^{-1}); MAI$_W$: mean annual increment in above-stump woody (STEM + BRANCH) biomass (Mg ha^{-1} year^{-1}); pFT: Ratio of FOLIAGE to TAGB.
Ranges are presented for sites with replications and multiple treatments.
[a] Site where data used for model fitting was collected. Stand-level data was not available for Albaugh (unpublished); Baldwin et al. (1997), Garbett (1977), Gibson et al. (1985), Manis (1977) and USFS (unpublished).
[b] Same site as Jokela and Martin (2000). Use the same biomass equations.
[c] Same site as Van Lear et al. (1984). Use the same biomass equations.
[d] Use equations from Swindel et al. (1979).

$$BRANCH = f_1 \cdot (dbh^{f_2}) \cdot \exp(f_3 \cdot dbh) \cdot (H^{f_4}) \cdot (AGE^{f_5}) \cdot (N^{f_6}) \cdot (BA^{f_7}) + \varepsilon_i \tag{26}$$

$$STEM, TASB = f_1 \cdot (dbh^{f_2}) \cdot (H^{f_3}) \cdot (AGE^{f_4}) \cdot (N^{f_5}) \cdot (Dp^{f_6}) + \varepsilon_i \tag{27}$$

$$BFRAC = \exp(f_1 + f_2 \cdot \ln(dbh^2 \cdot H) + f_3 \cdot Dp) + \varepsilon_i \tag{28}$$

For slash pine, the general models selected were:

$$FOLIAGE = f_1 \cdot (dbh^{f_2}) \cdot \exp(f_3 \cdot dbh) \cdot (H^{f_4}) \cdot (AGE^{f_5}) \cdot (N^{f_6}) \cdot (Dp^{f_7}) + \varepsilon_i \tag{29}$$

$$BRANCH = f_1 \cdot (dbh^{f_2}) \cdot (H^{f_3}) \cdot (AGE^{f_4}) \cdot (Dp^{f_5}) + \varepsilon_i \tag{30}$$

$$TASB, STEM = f_1 \cdot (dbh^{f_2}) \cdot (H^{f_3}) \cdot (AGE^{f_4}) \cdot (N^{f_5}) \cdot (Dp^{f_6}) + \varepsilon_i \tag{31}$$

$$BFRAC = \exp(f_1 + f_2 \cdot \ln(dbh^2 \cdot H) + f_3 \cdot \ln(Dq) + f_4 \cdot Dp) + \varepsilon_i \tag{32}$$

where f_1 to f_7 are curve fit parameter estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$. Note that for slash pine, the second parameter estimate for dbh was not significant in the model to estimate BRANCH.

2.3. Model fitting and evaluation

All statistical analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA). For all parameter estimates reported, non-linear model fitting was carried out using the procedure proc nlin. Logarithmic transformation of the response variable was carried out to determine the stand-level attributes to be included in the final general model. Once the explanatory variables were selected using the procedure proc reg, non-linear model fitting was carried out using the non-transformed variables. As 97% of sampling plots had three or less trees, we assumed that trees were taken from spatially independent locations and plot effect was not considered in data analysis. The predictive ability of all equations was evaluated by using a 10-fold cross validation (Neter et al., 1996), where the dataset was randomly split into 10 subsets with approximately equal numbers of observations. 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). As non-linear model fitting was carried out, an empirical R^2 (Myers, 2000) was determined as:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t} \tag{33}$$

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.

For both species, the equations for above-stump biomass were also compared against other models reported in the literature. For loblolly pine, the models used were reported by White and Pritchett (1970), Taras and Clark (1975), Van Lear et al. (1984), Baldwin (1987), Pienaar et al. (1996), Naidu et al. (1998), Jokela and Martin (2000) and Jenkins et al. (2003). For slash pine, the models tested were reported by White and Pritchett (1970), Taras and Phillips (1978), Swindel et al. (1979), Gholz and Fisher (1982), Lohrey (1984), Pienaar et al. (1987), Jokela et al. (1989) and Jokela and Martin (2000). The functions reported by Pienaar et al. (1987, 1996) only allowed estimation of stem wood inside bark biomass, but they provided a good comparison as they were fitted to a large dataset, covering multiple sites across the southeastern U.S. After splitting the whole dataset into three dbh classes (<10 cm, 10–20 cm, >20 cm), mean bias error was computed for each biomass component within each dbh class and compared against two of the fitted models: a local model (using only dbh as explanatory variable) and a general model (using dbh, H, AGE

Table 4
Summary of data of published functions used for comparison for loblolly and slash pine above-stump biomass.

Species	Reference	n	AGE (yrs.)	dbh (cm)	H (m)	Equation form	Stand type	Geographic source
Loblolly	White and Pritchett (1970)[a]	54	5	3.2–6.8	2.0–4.2	$\log_{10}Y = a + b \cdot \log_{10} (dbh) + c \cdot \log_{10} (H)$	Planted	Florida Flatwoods
	Taras and Clark (1975)[a]	41	31–47	14.2–51.8	14.6–32.6	$\log_{10}Y = a + b \cdot \log_{10} (dbh^2 \cdot H)$	Natural	Central Alabama
	Van Lear et al. (1984)[a]	16	41	12.7–38.6	15.6–25.4	$\log_{10}Y = a + b \cdot \log_{10} (dbh)$	Planted	South Carolina Piedmont
	Baldwin (1987)	130	9–55	5.1–53.3	5.5–28.7	$\ln Y = a + b \cdot \ln(dbh) + c \cdot \ln(H)$	Planted	West Gulf Region
	Jenkins et al. (2003)[a]	331[c]	n.a.	5.0–80.0	n.a.	$Y = \exp(a + b \cdot \ln(dbh)) Y = \exp(a + b/dbh)$	Planted / natural	Southeast U.S. Wide
	Naidu et al. (1998)	15[d]	7–45	6.5–35.6	4.8–23.0	$\log_{10}Y = a + b \cdot \log_{10} (dbh)$	Planted	North Carolina Piedmont
	Jokela and Martin (2000)	40	13	9.0–25.2	8.7–19.0	$\ln Y = a + b \cdot \ln(dbh^2)$	Planted	Florida Flatwoods
	Pienaar et al. (1987)[b]	832	6–30	5.1–35.6	4.6–25.9	$Y = a \cdot dbh^b \cdot H^c \cdot Age^d$	Planted	Lower Coastal Plain
Slash	White and Pritchett (1970)[a]	54	5	3.2–6.8	2.0–4.2	$\log_{10}Y = a + b \cdot \log_{10} (dbh) + c \cdot \log_{10} (H)$	Planted	Florida Flatwoods
	Taras and Phillips (1978)[a]	43	28–68	15.7–53.3	14.3–30.2	$\log_{10}Y = a + b \cdot \log_{10} (dbh^2 \cdot H)$	Natural	Southern Alabama
	Swindel et al. (1979)	128	n.a.	5.0–35.5	n.a.	$\ln Y = a + b \cdot \ln(dbh)$	Natural	Florida Flatwoods
	Gholz and Fisher (1982)[a]	19[d]	5–34	4.2–20.0	3.5–19.7	$\ln Y = a + b \cdot \ln(dbh)$	Planted	Florida Flatwoods
	Lohrey (1984)[a]	201	12–48	5.6–48.5	6.1–33.5	$\ln Y = a + b \cdot \ln(dbh) + c \cdot \ln(H)$	Planted	Western Gulf Region
	Jenkins et al. (2003)[a]	331[c]	n.a.	5.0–80.0	n.a.	$Y = \exp(a + b \cdot \ln(dbh)) Y = \exp(a + b/dbh)$	Planted / natural	Southeast U.S. Wide
	Jokela and Martin (2000)	40	13	10.2–24.2	8.7–17.6	$\ln Y = a + b \cdot \ln(dbh^2)$	Planted	Florida Flatwoods
	Pienaar et al. (1996)[b]	838	9–27	7.6–35.6	6.1–22.9	$Y = a \cdot dbh^b \cdot H^c \cdot Age^d$	Planted	Southern Coastal Plain

n: number of observations; AGE: range of age of measured trees (yrs.); dbh: range of dbh of measured trees (cm); H: range of height of measured trees (m).
[a] Used also for FBRAC comparisons.
[b] Used only for WOOD comparisons.
[c] Use of data points generated from published equations (Naidu et al., 1998; Nelson and Swittzer, 1975; Ralston, 1973 and Van Lear et al., 1984) at 5 cm intervals. Not true sampling.
[d] Only for dominant trees.

and stand parameters). A description of the dataset used for each of the references listed above is shown in Table 4.

3. Results

The model parameter estimates for the selected local and general functions to estimate above-stump biomass for loblolly and slash pine trees growing in the southeastern U.S. are reported in Table 5 (BRANCH, BR), Table 6 (FOLIAGE, F), Table 7 (STEM, S), Table 8 (TASB, T) and Table 9 (BFRAC, BF). Models were labeled using the abbreviations previously described for each biomass component, including a number that identifies the equation set. For example, BR1 corresponds to an equation for BRANCH that uses the set of equations 1 (only use dbh as predictor), or BF6 corresponds to an equation for BFRAC that uses the set of equations 6 (use dbh, H, AGE and other stand attributes as predictors). All parameter estimates were significant at $P < 0.05$.

3.1. Model fitting

For loblolly pine, the local model that estimated BRANCH biomass using only dbh (local model BR1) showed little improvement when H (local model BR4) was included (Table 5). In the case of slash pine, the local model that estimated BRANCH biomass using only dbh (local model BR1) was highly improved when H was included (local model BR4), reducing the RMSE and CV by about 10%. For both species, when AGE was added (general model BR2), the fit of the models improved, reducing the RMSE and coefficient of variation (CV) by about 5%. The general models BR3 and BR6 (that included stand parameters) showed the best fit (Table 5). For both species, the parameter estimate for AGE was always negative, implying that for the same size (dbh or dbh and H), older

trees had less living branches than younger trees. When significant in the model, the parameter estimate for N was always negative, implying that for the same size (dbh or dbh and H) and AGE, trees growing in stands with more trees (more intraspecific competition) had less and/or smaller size living branches than trees growing in stands with less intraspecific competition. In the case of the parameter estimate Dp, when significant in the model, it was always positive, implying that for the same size (dbh or dbh and H) and stand conditions (stocking and AGE), dominant trees with dbh larger than Dq had more branches than trees with dbh smaller than Dq. For slash pine trees, the parameter estimate for H was always negative, implying that for the same dbh, AGE and stand conditions (stocking and productivity), taller slash pine trees had less living branch biomass than shorter trees. For loblolly pine, in the absence of stand variables, the parameter estimate for H was negative, indicating that, on average, a taller tree of the same dbh (that can be an older tree or a tree growing in a more productive site or in a site with more trees competing), will have less living branch biomass than shorter trees of the same dbh, but when stand variables (AGE, N and BA) are known, for the same dbh and stand conditions, a taller loblolly pine tree would have more living branch biomass than a shorter tree.

For both species, the models that estimated FOLIAGE biomass showed little improvement when H and AGE were included (Table 6). For both species, when H was unknown, the general model F3 (that included dbh, AGE, N and Dp) showed the best fit (RMSE and CV was about 10% lower than the best local model), being similar to the general model F6 that used dbh, H, AGE and N (Dp was not significant when H was known). In all cases, the R^2 was larger than 0.87 (Table 6). Similar to BRANCH, the parameter estimate for AGE was always negative, implying that for the same size, older trees had less living needle biomass than younger trees. The parameter estimate for N was always negative, implying

Table 5
Parameter estimates and fit statistics of the selected biomass functions to estimate total living branch biomass (BRANCH) for loblolly and slash pine trees growing in southeastern U.S.

Species	Model ID	Model	Parameter	Parameter estimate	SE	R^2	RMSE	CV%
Loblolly	BR1	$= a_1 \cdot (\text{dbh}^{a_2}) \cdot (e^{a_3 \cdot \text{dbh}})$	a_1	0.080677	0.035879	0.887	4.09	65.1
			a_2	1.470995	0.213834			
			a_3	0.046861	0.009640			
	BR2	$= b_1 \cdot (\text{dbh}^{b_2}) \cdot (e^{b_3 \cdot \text{dbh}})(\text{AGE}^{b_4})$	b_1	0.064984	0.027319	0.898	3.88	61.8
			b_2	1.810409	0.207192			
			b_3	0.050342	0.009159			
			b_4	−0.334387	0.037499			
	BR3	$= c_1 \cdot (\text{dbh}^{c_2}) \cdot (e^{c_3 \cdot \text{dbh}}) \cdot (\text{AGE}^{c_4}) \cdot (\text{N}^{c_5}) \cdot (\text{BA}^{c_6})$	c_1	0.001489	0.000901	0.905	3.61	62.1
			c_2	2.666856	0.268414			
			c_3	0.031849	0.011158			
			c_4	−0.228985	0.040927			
			c_5	0.38328	0.054412			
			c_6	−0.423839	0.049285			
	BR4	$= d_1 \cdot (\text{dbh}^{d_2}) \cdot (e^{d_3 \cdot \text{dbh}}) \cdot (H^{d_4})$	d_1	0.066038	0.030267	0.888	4.07	70.1
			d_2	1.782699	0.250249			
			d_3	0.041284	0.010000			
			d_4	−0.230006	0.090922			
	BR5	$= e_1 \cdot (\text{dbh}^{e_2}) \cdot (e^{e_3 \cdot \text{dbh}}) \cdot (H^{e_4}) \cdot (\text{AGE}^{e_5})$	e_1	0.075259	0.031589	0.899	3.88	61.7
			e_2	1.599282	0.235330			
			e_3	0.055050	0.009391			
			e_4	0.179042	0.050158			
			e_5	−0.369679	0.042700			
	BR6	$= f_1 \cdot (\text{dbh}^{f_2}) \cdot (e^{f_3 \cdot \text{dbh}}) \cdot (H^{f_4}) \cdot (\text{AGE}^{f_5}) \cdot (\text{N}^{f_6}) \cdot (\text{BA}^{f_7})$	f_1	0.001568	0.000907	0.910	3.51	60.4
			f_2	2.119937	0.261932			
			f_3	0.040940	0.010375			
			f_4	0.667628	0.106892			
			f_5	−0.352632	0.045653			
			f_6	0.414580	0.053242			
			f_7	−0.511470	0.050539			
Slash	BR1	$= a_1 \cdot (\text{dbh}^{a_2}) \cdot (e^{a_3 \cdot \text{dbh}})$	a_1	0.001902	0.001992	0.937	3.34	52.5
			a_2	3.119523	0.476125			
			a_3	−0.011604	0.019120			
	BR2	$= b_1 \cdot (\text{dbh}^{b_2}) \cdot (e^{b_3 \cdot \text{dbh}}) \cdot (\text{AGE}^{b_4})$	b_1	0.004742	0.003696	0.956	2.77	43.6
			b_2	3.036602	0.352601			
			b_3	0.022211	0.014520			
			b_4	−0.462590	0.044211			
	BR3	$= c_1 \cdot (\text{dbh}^{c_2}) \cdot (e^{c_3 \cdot \text{dbh}}) \cdot (\text{AGE}^{c_4}) \cdot (\text{Dp}^{c_5})$	c_1	0.002649	0.002083	0.961	2.62	41.2
			c_2	3.338326	0.354730			
			c_3	0.029490	0.014412			
			c_4	−0.604011	0.048727			
			c_5	−0.551667	0.101229			
	BR4	$= d_1 \cdot (\text{dbh}^{d_2}) \cdot (e^{d_3 \cdot \text{dbh}}) \cdot (H^{d_4})$	d_1	0.000765	0.000613	0.950	2.97	46.7
			d_2	4.927645	0.441610			
			d_3	−0.050347	0.015591			
			d_4	−1.334273	0.157841			
	BR5	$= e_1 \cdot (\text{dbh}^{e_2}) \cdot (H^{e_3}) \cdot (\text{AGE}^{e_4})$	e_1	0.002830	0.000691	0.959	2.70	42.4
			e_2	3.835417	0.115382			
			e_3	−0.610884	0.143477			
			e_4	−0.368834	0.045714			
	BR6	$= f_1 \cdot (\text{dbh}^{f_2}) \cdot (H^{f_3}) \cdot (\text{AGE}^{f_4}) \cdot (\text{Dp}^{f_5})$	f_1	0.001174	0.000360	0.963	2.57	40.4
			f_2	4.252145	0.137345			
			f_3	−0.586573	0.143641			
			f_4	−0.500808	0.050010			
			f_5	−0.492377	0.095096			

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dp: ratio between dbh and quadratic mean diameter (cm cm^{-1}); BRANCH: total living branch biomass (kg); SE: standard error; R^2: coefficient of determination; RMSE: root mean square error (kg); CV: coefficient of variation (100 RMSE/mean). For all parameter estimates $P < 0.05$.

that for the same size and AGE, trees growing in stands with more intraspecific competition had less living needle biomass than trees growing in stands with less intraspecific competition. When significant in the model, the parameter estimate for Dp was always positive, implying that for the same size, AGE and stand conditions (stocking and productivity), dominant trees had more living needle biomass than suppressed trees. For both species, the parameter estimates for H were always negative, implying that for the same dbh and stand conditions (AGE, stocking and productivity), taller trees had less living needle biomass than shorter trees.

For STEM biomass with both species, the local model S1 (that used only dbh) improved highly when H was included (local model

S4; RMSE and CV were reduced by more than 40%). When H was unknown, stand variables did not significantly improve the model fit (general models S2 and S3), but when H was known, stand variables continue improving the fit (general models S5 and S6), having a RMSE and CV 50% lower than the local model that relied only on dbh. For both species, the general model that showed the best fit included dbh, H, AGE, N and Dp (general model S6). In all cases, the R^2 was larger than 0.95 (Table 7). Contrary to FOLIAGE, the parameter estimate for H was always positive, implying that for the same dbh and stand conditions (AGE, stocking and productivity), taller trees had more above stump stem over bark biomass (and volume) than shorter trees. In the absence of H in the model,

Table 6

Parameter estimates and fit statistics of the selected biomass functions to estimate total living needles biomass (FOLIAGE) for loblolly and slash pine trees growing in southeastern U.S.

Species	Model ID	Model	Parameter	Parameter estimate	SE	R^2	RMSE	CV%
Loblolly	F1	$= a_1 \cdot (dbh^{a_2}) \cdot (e^{a_3 \cdot dbh})$	a_1	1.045339	0.124596	0.870	1.70	48.9
			a_2	0.142074	0.069218			
			a_3	0.071915	0.004556			
	F2	$= b_1 \cdot (dbh^{b_2}) \cdot (e^{b_3 \cdot dbh})(AGE^{b_4})$	b_1	0.931666	0.105237	0.901	1.48	46.6
			b_2	0.557249	0.070103			
			b_3	0.080807	0.004258			
			b_4	−0.507671	0.034305			
	F3	$= c_1 \cdot (dbh^{c_2}) \cdot (e^{c_3 \cdot dbh}) \cdot (AGE^{c_4}) \cdot (N^{c_5}) \cdot (Dp^{c_6})$	c_1	4.943520	1.748127	0.889	1.54	44.3
			c_2	0.707327	0.079251			
			c_3	0.058378	0.005648			
			c_4	−0.467468	0.036795			
			c_5	−0.254560	0.049416			
			c_6	0.302643	0.065338			
	F4	$= d_1 \cdot (dbh^{d_2}) \cdot (e^{d_3 \cdot dbh}) \cdot (H^{d_4})$	d_1	0.992060	0.124457	0.870	1.70	53.6
			d_2	0.907561	0.095031			
			d_3	0.070654	0.004469			
			d_4	−0.835076	0.068463			
	F5	$= e_1 \cdot (dbh^{e_2}) \cdot (e^{e_3 \cdot dbh}) \cdot (H^{e_4}) \cdot (AGE^{e_5})$	e_1	0.923902	0.108254	0.901	1.48	46.6
			e_2	0.862958	0.090054			
			e_3	0.078592	0.004289			
			e_4	−0.438251	0.077224			
			e_5	−0.391617	0.038487			
	F6	$= f_1 \cdot (dbh^{f_2}) \cdot (e^{f_3 \cdot dbh}) \cdot (H^{f_4}) \cdot (AGE^{f_5}) \cdot (N^{f_6}) \cdot (Dp^{f_7})$	f_1	3.746583	1.358997	0.903	1.44	45.4
			f_2	0.883835	0.097412			
			f_3	0.062461	0.005769			
			f_4	−0.284381	0.091178			
			f_5	−0.413381	0.039879			
			f_6	−0.212743	0.050897			
			f_7	0.174500	0.075860			
Slash	F1	$= a_1 \cdot (dbh^{a_2}) \cdot (e^{a_3 \cdot dbh})$	a_1	0.762985	0.207715	0.912	2.19	50.6
			a_2	0.193582	0.033806			
			a_3	0.090734	0.006475			
	F2	$= b_1 \cdot (dbh^{b_2}) \cdot (e^{b_3 \cdot dbh}) \cdot (AGE^{b_4})$	b_1	0.774927	0.181310	0.925	2.03	46.9
			b_2	0.451519	0.121691			
			b_3	0.103928	0.006333			
			b_4	−0.352839	0.055053			
	F3	$= c_1 \cdot (dbh^{c_2}) \cdot (e^{c_3 \cdot dbh}) \cdot (AGE^{c_4}) \cdot (BA^{c_5})$	c_1	0.513984	0.153334	0.926	2.01	46.5
			c_2	0.886721	0.227072			
			c_3	0.087011	0.009691			
			c_4	−0.379107	0.056287			
			c_5	−0.148298	0.064028			
	F4	$= d_1 \cdot (dbh^{d_2}) \cdot (e^{d_3 \cdot dbh}) \cdot (H^{d_4})$	d_1	0.636083	0.174914	0.914	2.16	50.0
			d_2	0.678960	0.220352			
			d_3	−0.407499	0.144974			
			d_4	0.084191	0.006909			
	F5	$= e_1 \cdot (dbh^{e_2}) \cdot (H^{e_3}) \cdot (AGE^{e_4})$	e_1	0.006913	0.003331	0.888	2.47	57.3
			e_2	2.812268	0.172642			
			e_3	−0.293182	0.303172			
			e_4	−0.137734	0.081649			
	F6	$= f_1 \cdot (dbh^{f_2}) \cdot (e^{f_3 \cdot dbh}) \cdot (H^{f_4}) \cdot (AGE^{f_5}) \cdot (BA^{f_6}) \cdot (Dp^{f_7})$	f_1	0.216725	0.063532	0.942	1.78	41.1
			f_2	1.277811	0.232734			
			f_3	0.095650	0.008676			
			f_4	1.140021	0.204587			
			f_5	−1.083902	0.102263			
			f_6	−0.610551	0.084444			
			f_7	−1.118487	0.154301			

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dp: ratio between dbh and quadratic mean diameter (cm cm^{-1}); FOLIAGE: total living needles biomass (kg); SE: standard error; R^2: coefficient of determination; RMSE: root mean square error (kg); CV: coefficient of variation (100 RMSE/mean). For all parameter estimates $P < 0.05$.

the parameter estimate for AGE was always positive, indicating that for the same dbh, and stand conditions (stocking and productivity), older trees had more above stump stem over bark biomass than younger trees. Trees of the same dbh, H and AGE growing in highly stocked stands (larger N), had less STEM biomass than trees growing in more open stands.

The models to estimate TASB followed a similar fitting behavior as STEM. For both species, the models that included H had a better fit than those models that only used dbh or dbh and stand variables. For both species, the general model that showed the best

fit included dbh, H, AGE, N and Dp (general model T6). In all cases, the R^2 was greater than 0.96 (Table 8). Similar to STEM, the parameter estimate for H was, as expected, always positive, implying that for the same dbh, AGE and stand conditions, taller trees would have more total above-stump biomass than shorter trees. For loblolly pine trees, in the absence of H, the parameter estimate associated with AGE was non-significant. On the other hand, for slash pine trees, the parameter estimate for AGE was always significant, indicating different ontogeny effect on TASB allometry for both species.

Table 7
Parameter estimates and fit statistics of the selected functions to estimate above stump stem over bark biomass (STEM) for loblolly and slash pine trees growing in southeastern U.S.

Species	Model ID	Model	Parameter	Parameter Estimate	SE	R^2	RMSE	CV%
Loblolly	S1	$= a_1 \cdot (\text{dbh}^{a_2})$	a_1	0.021754	0.001984	0.959	12.55	43.2
			a_2	2.774428	0.027948			
	S2	$= b_1 \cdot (\text{dbh}^{b_2}) \cdot (\text{AGE}^{b_3})$	b_1	0.023553	0.002221	0.960	12.49	43.0
			b_2	2.689207	0.040330			
			b_3	0.067017	0.023220			
	S3	$= c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{BA}^{c_3})$	c_1	0.024109	0.002630	0.959	12.53	43.2
			c_2	2.793817	0.030230			
			c_3	−0.048782	0.019901			
	S4	$= d_1 \cdot (\text{dbh}^{d_2}) \cdot (H^{d_3})$	d_1	0.012591	0.000805	0.985	7.59	26.1
			d_2	1.816703	0.029766			
			d_3	1.260939	0.036319			
	S5	$= e_1 \cdot (\text{dbh}^{e_2}) \cdot (H^{e_3}) \cdot (\text{AGE}^{e_4})$	e_1	0.010244	0.000630	0.988	6.94	23.9
			e_2	1.874136	0.028160			
			e_3	1.448326	0.037085			
			e_4	−0.177850	0.014971			
	S6	$= f_1 \cdot (\text{dbh}^{f_2}) \cdot (H^{f_3}) \cdot (\text{AGE}^{f_4}) \cdot (N^{f_5}) \cdot (\text{Dp}^{f_6})$	f_1	0.088273	0.018557	0.989	6.23	21.4
			f_2	1.497337	0.043329			
			f_3	1.462580	0.036712			
			f_4	−0.160971	0.015070			
			f_5	−0.160969	0.018428			
			f_6	0.383145	0.036992			
Slash	S1	$= a_1 \cdot (\text{dbh}^{a_2})$	a_1	0.030328	0.004045	0.970	14.43	37.4
			a_2	2.759097	0.040921			
	S2	$= b_1 \cdot (\text{dbh}^{b_2}) \cdot (\text{AGE}^{b_3})$	b_1	0.051774	0.004899	0.983	10.6	27.5
			b_2	2.242298	0.041829			
			b_3	0.339722	0.022543			
	S3	$= c_1 \cdot (\text{dbh}^{c_2}) \cdot (\text{AGE}^{c_3}) \cdot (N^{c_4})$	c_1	0.020998	0.005969	0.984	10.4	27.0
			c_2	2.261548	0.041587			
			c_3	0.413991	0.031106			
			c_4	0.089978	0.026503			
	S4	$= d_1 \cdot (\text{dbh}^{d_2}) \cdot (H^{d_3})$	d_1	0.004940	0.000705	0.988	9.09	23.6
			d_2	1.827196	0.051032			
			d_3	1.630634	0.085398			
	S5	$= e_1 \cdot (\text{dbh}^{e_2}) \cdot (H^{e_3}) \cdot (\text{AGE}^{e_4})$	e_1	0.010422	0.001518	0.991	7.92	20.5
			e_2	1.790921	0.043818			
			e_3	1.209111	0.087289			
			e_4	0.185100	0.020138			
	S6	$= f_1 \cdot (\text{dbh}^{f_2}) \cdot (H^{f_3}) \cdot (\text{AGE}^{f_4}) \cdot (N^{f_5}) \cdot (\text{Dp}^{f_6})$	f_1	0.126250	0.033294	0.994	6.63	17.2
			f_2	1.106372	0.074002			
			f_3	1.712652	0.090604			
			f_4	0.062995	0.028124			
			f_5	−0.226469	0.023657			
			f_6	0.548775	0.057279			

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dp: ratio between dbh and quadratic mean diameter (cm cm^{-1}); STEM: above stump stem over bark biomass (kg); SE: standard error; R^2: coefficient of determination; RMSE: root mean square error (kg); CV: coefficient of variation (100 RMSE/mean). For all parameter estimates $P < 0.05$.

For BFRAC with both species, model fitting showed little improvement when stand variables were included (Table 9). The incorporation of H into the model produced the largest improvements in the model fit. When H was unknown, the model that used dbh and AGE (general model BF2) improved the fit, being intermediate between the local model that only used dbh (local model BF1) and the local model that used dbh and H (local model BF4). For loblolly pine, the general model that showed the best fit included dbh$^2 \cdot$H and Dp (general model BF6). On the other hand, for slash pine, there were no differences in model fitting between the general model BF5 (which included dbh$^2 \cdot$H and AGE) and BF6 (which included dbh$^2 \cdot$H, Dq and Dp). The negative sign of the parameters estimates for dbh, dbh$^2 \cdot$H and AGE indicates that as the trees get bigger and/or older, the proportion of bark biomass relative to stem over-bark biomass was reduced. When significant in the model, the parameter estimate for Dp was positive for both species, indicating that, for the same size, a tree growing in a stand with a larger Dq (maybe due to larger BA or lower N) would have more bark biomass relative to stem over-bark biomass when compared to a tree growing in a stand with a smaller Dq.

3.2. Model evaluation

Fig. 4 (loblolly pine) and Fig. 5 (slash pine) show examples of model evaluation for all biomass components analyzed (estimated WOOD and BARK were computed using the models for STEM and BFRAC). For a clearer exposition of the results we show graphically the local models that used only dbh as an explanatory variable (labeled as Local Model in figure legend) and the general models described in equation set 6, that used dbh, H, AGE and stand variables (labeled as General Model in figure legend). In addition, Table 10 shows a summary of the model performance test using a 10-fold cross validation for all selected local and general models fitted for both species.

For loblolly pine, the relationship between predicted and observed values for FOLIAGE using the local model based on dbh (local model F1; Fig. 4a), showed a tendency to underestimate the results for trees with FOLIAGE larger than about 10 kg. When the variables AGE, N and Dp were included in the model the relationship improved (general model F6; Fig. 4a). On the other hand, for slash pine there was no clear tendency to over or underestimate

Table 8
Parameter estimates and fit statistics of the selected functions to estimate total above-stump biomass (TASB) for loblolly and slash pine trees growing in southeastern U.S.

Species	Model ID	Model	Parameter	Parameter Estimate	SE	R2	RMSE	CV%
Loblolly	T1	$= a_1 \cdot (dbh^{a_2})$	a_1	0.037403	0.002947	0.969	13.68	35.3
			a_2	2.676835	0.024240			
	T2	$= b_1 \cdot (dbh^{b_2}) \cdot (AGE^{b_3})$	b_3 non-significant					
	T3	$= c_1 \cdot (dbh^{c_2}) \cdot (N^{c_3}) \cdot (Dp^{c_4})$	c_1	0.093954	0.029520	0.970	12.94	33.4
			c_2	2.498865	0.044215			
			c_3	−0.057304	0.028947			
			c_4	0.227395	0.054333			
	T4	$= d_1 \cdot (dbh^{d_2}) \cdot (H^{d_3})$	d_1	0.026256	0.001787	0.982	10.50	27.1
			d_2	2.015144	0.033168			
			d_3	0.864052	0.038985			
	T5	$= e_1 \cdot (dbh^{e_2}) \cdot (H^{e_3}) \cdot (AGE^{e_4})$	e_1	0.020594	0.001344	0.985	9.50	24.5
			e_2	2.082279	0.031123			
			e_3	1.081437	0.039692			
			e_4	−0.205654	0.016261			
	T6	$= f_1 \cdot (dbh^{f_2}) \cdot (H^{f_3}) \cdot (AGE^{f_4}) \cdot (N^{f_5}) \cdot (Dp^{f_6})$	f_1	0.347585	0.071048	0.988	8.06	20.8
			f_2	1.515726	0.043537			
			f_3	1.179694	0.036662			
			f_4	−0.183786	0.015448			
			f_5	−0.214381	0.018600			
			f_6	0.591226	0.036832			
Slash	T1	$= a_1 \cdot (dbh^{a_2})$	a_1	0.041281	0.004282	0.982	13.47	27.3
			a_2	2.722214	0.031862			
	T2	$= b_1 \cdot (dbh^{b_2}) \cdot (AGE^{b_3})$	b_1	0.057836	0.005159	0.987	11.4	23.2
			b_2	2.407877	0.039554			
			b_3	0.203611	0.020405			
	T3	$= c_1 \cdot (dbh^{c_2}) \cdot (AGE^{c_3}) \cdot (Dp^{c_4})$	c_1	0.067849	0.009005	0.987	11.4	23.2
			c_2	2.325341	0.06479			
			c_3	0.228687	0.025815			
			c_4	0.101174	0.043139			
	T4	$= d_1 \cdot (dbh^{d_2}) \cdot (H^{d_3})$	d_1	0.013008	0.001644	0.990	10.12	20.5
			d_2	2.119503	0.048208			
			d_3	1.048906	0.078083			
	T5	$= e_1 \cdot (dbh^{e_2}) \cdot (H^{e_3}) \cdot (AGE^{e_4})$	e_1	0.067849	0.009005	0.991	9.78	19.8
			e_2	2.325341	0.06479			
			e_3	0.228687	0.025815			
			e_4	0.101174	0.053139			
	T6	$= f_1 \cdot (dbh^{f_2}) \cdot (H^{f_3}) \cdot (AGE^{f_4}) \cdot (N^{f_5}) \cdot (Dp^{f_6})$	f_1	0.226275	0.062172	0.993	8.27	16.7
			f_2	1.465187	0.076758			
			f_3	1.394051	0.094606			
			f_4	−0.077625	0.029785			
			f_5	−0.244804	0.025076			
			f_6	0.469951	0.058105			

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dp: ratio between dbh and quadratic mean diameter (cm cm^{-1}); TASB: total above-stump biomass (kg); SE: standard error; R^2: coefficient of determination; RMSE: root mean square error (kg); CV: coefficient of variation (100 RMSE/mean). For all parameter estimates $P < 0.05$.

FOLIAGE (Fig. 5a). Model performance tests indicated that FOLIAGE estimates agreed better with observed values when the stand variables were included, as occurs in the general models (Table 10). For example, with loblolly pine the RMSE and Bias were reduced from 54.8% and 6.6% (model F1) to 46.5% and 4.1% (model F3), respectively, and the R² increased from 0.642 to 0.752, respectively. When H was included in the local model (local model F4) an improvement in the model performance was noted, but when AGE was included in the general model F5 the results were similar between models F1 and F4 (Table 10). Interestingly, the variable allometric ratio model (local model F2) improved, for loblolly, the accuracy and precision of the local model, reducing the Bias from 6.6% to 0.3%, and the RMSE from 54.8% to 49.2%. In the case of slash pine the improvement due to model F2 was even larger, reducing the Bias from 17.2% to 0.1% and the RMSE from 63.6% to 52.3%.

For both species, the relationship between predicted and observed values for BARK, WOOD and STEM showed no tendency to over or underestimate the results (Fig. 4b, d and f, loblolly; Fig. 5b, d and f, slash). For BFRAC and STEM, there was a large improvement in agreement between the estimated and observed values when H was included in the models. For example, for slash pine BFRAC, the RMSE and Bias were reduced from 18.5% and −0.5% (model BF1) to 15.4% and −0.4% (model BF4), respectively; the R² increased from 0.746 to 0.823, respectively (Table 10). For slash pine STEM, the RMSE reduced from 40.9% (model S1) to 26.2% (model S4) and 19.6% (model S6). In general, the R² was greater than 0.95 (Table 10). For BFRAC, when H was unknown, AGE alone could be used as a surrogate of H, as the general models BF2 showed a similar RMSE and Bias than the local models BF4. When H was known, inclusion of stand variables showed little improvement in model performance.

The relationship between predicted and observed values for BRANCH presented, for both species, showed no tendency to over or underestimate (Fig. 4c, loblolly; Fig. 5c, slash). Larger improvement in model performance was observed when the stand variables were included in the model and H showed little effect on model performance. For example, for loblolly pine the RMSE reduced from 53.6% (model B1) to 44.6% (model B4) and 40.4% (model B6), and the R² increased from 0.915 to 0.941 and 0.952, respectively (Table 10).

The relationship between predicted and observed values for TASB (Fig. 4e, loblolly; Fig. 5e, slash) showed no tendency to over or underestimate. Larger improvements in model performance

Table 9

Parameter estimates and fit statistics of the selected functions to estimate bark to stem over-bark biomass fraction (BFRAC) for loblolly and slash pine trees growing in southeastern U.S.

Species	Model ID	Model	Parameter	Parameter estimate	SE	R^2	RMSE	CV%
Loblolly	BF1	$e^{(a_1+a_2\cdot\ln(dbh))}$	a_1	−0.741527	0.037278	0.976	0.028	16.1
			a_2	−0.436613	0.017082			
	BF2	$e^{(b_1+b_2\cdot\ln(dbh)+b_3\cdot AGE)}$	b_1	−0.758061	0.037347	0.978	0.027	15.5
			b_2	−0.397302	0.019462			
			b_3	−0.009705	0.002463			
	BF3	$e^{(c_1+c_2\cdot\ln(dbh)+c_3\cdot\ln(Dq))}$	c_1	−0.648318	0.045179	0.977	0.027	15.7
			c_2	−0.329283	0.037683			
			c_3	−0.145688	0.044932			
	BF4	$e^{(d_1+d_2\cdot\ln(dbh^2\cdot H))}$	d_1	−0.702268	0.034831	0.981	0.025	14.6
			d_2	−0.157165	0.005561			
	BF5	$e^{(e_1+e_2\cdot\ln(dbh^2\cdot H)+e_3\cdot AGE)}$	e_1	−0.713782	0.036020	0.981	0.025	14.6
			e_2	−0.151319	0.006764			
			e_3	−0.003605	0.001355			
	BF6	$e^{(f_1+f_2\cdot\ln(dbh^2\cdot H)+f_3\cdot Dp)}$	f_1	−0.765819	0.044018	0.981	0.025	14.4
			f_2	−0.165263	0.006439			
			f_3	0.117441	0.049080			
Slash	BF1	$e^{(a_1+a_2\cdot\ln(dbh))}$	a_1	−0.187112	0.056402	0.971	0.042	17.9
			a_2	−0.524506	0.025514			
	BF2	$e^{(b_1+b_2\cdot\ln(dbh)+b_3\cdot AGE)}$	b_1	−0.315992	0.053477	0.980	0.036	15.1
			b_2	−0.374368	0.031478			
			b_3	−0.022298	0.003504			
	BF3	$e^{(c_1+c_2\cdot\ln(dbh)+c_3\cdot AGE+c_4\cdot\ln(N))}$	c_1	1.185880	0.477950	0.981	0.034	14.6
			c_2	−0.378673	0.030271			
			c_3	−0.024159	0.003389			
			c_4	−0.203351	0.064442			
	BF4	$e^{(d_1+d_2\cdot\ln(dbh^2\cdot H))}$	d_1	−0.202268	0.044715	0.980	0.035	14.9
			d_2	−0.179306	0.007068			
	BF5	$e^{(e_1+e_2\cdot\ln(dbh^2\cdot H)+e_3\cdot AGE)}$	e_1	−0.118209	0.061814	0.983	0.033	13.8
			e_2	−0.404459	0.057699			
			e_3	−0.147821	0.063678			
	BF6	$e^{(f_1+f_2\cdot\ln(dbh^2\cdot H)+f_3\cdot\ln(Dq)+f_4\cdot Dp)}$	f_1	−1.174585	0.207040	0.983	0.033	13.8
			f_2	−0.459350	0.058307			
			f_3	0.881355	0.182556			
			f_4	0.775490	0.165508			

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dq: quadratic mean diameter (cm); Dp: ratio between dbh and Dq (cm cm^{-1}); BFRAC: bark to stem over-bark biomass fraction (kg kg^{-1}); SE: standard error; R^2: coefficient of determination; RMSE: root mean square error (kg kg^{-1}); CV: coefficient of variation (100 RMSE/mean). For all parameter estimates $P < 0.05$.

were observed when H and stand variables were included. For example, for loblolly pine TASB, the RMSE was reduced from 37.0% (model T1) to 25.8 (model T4) and 23.6% (model T6). In general, the R^2 was greater than 0.95 (Table 10).

3.3. Comparison against published equations

Predicted values of the models in this study for all components of above-stump biomass were within the range of variation for estimations using other published equations for loblolly and slash pine trees. The effects of tree dbh on the above-stump estimations for several models are presented in Table 11 (loblolly pine) and Table 12 (slash pine).

For loblolly pine trees with dbh smaller than 10 cm, TASB was better predicted by the models of Jokela and Martin (2000) and Naidu et al. (1998), while the model of Taras and Clark (1975) and White and Pritchett (1970) provided poorer predictions. The general model T6 presented in this study produced the RMSE and Bias slightly larger than the better models of Jokela and Martin (2000) and Naidu et al. (1998). The model of Van Lear et al. (1984) for TASB produced the lowest Bias (2.8%), but had a large RMSE (45.4%). The other reported models (Baldwin, 1987 and Jenkins et al., 2003) presented intermediate prediction ability (Table 11). In the case of FOLIAGE, the general model F6 presented in this study produced the best predictions, followed closely by the model of Baldwin (1987). Other models such as Jenkins et al. (2003), Taras and Clark (1975) and Van Lear et al. (1984) estimated FOLIAGE with larger error, more than doubling the Bias and RMSE of

the best model from this study (Table 11). The estimates of BRANCH from the model of Jenkins et al. (2003) produced the lowest Bias and RMSE, followed closely by the model of Baldwin (1987), Jokela and Martin (2000) and the general model B6 from this study. Similar to FOLIAGE, the models of Taras and Clark (1975) and Van Lear et al. (1984) estimated BRANCH with larger error (Table 11). In the case of WOOD, the model of Taras and Clark (1975), White and Pritchett (1970) and the estimates of WOOD from the present study (using the general model BF6 and S6) showed the best predictions. The model of Van Lear et al. (1984) for WOOD produced the largest errors. The estimates of BARK from the present study (using the general model BF6 and S6) showed lower Bias and RMSE (7.3% and 32%, respectively). The model of Baldwin (1987) showed lower Bias but larger RMSE (Table 11).

For intermediate-sized loblolly pine trees with dbh between 10 and 20 cm, the general models from this study produced the best predictions, showing the lowest Bias and RMSE for all above-stump biomass components analyzed (Table 11). The model of White and Pritchett (1970) produced very large errors in the estimations of FOLIAGE. For loblolly pine trees with a dbh larger than 20 cm, the models presented in this study produced the best predictions for TASB, BRANCH, WOOD and STEM (Table 11). The model of Taras and Clark (1975) produced better estimates for FOLIAGE and the model of Jenkins et al. (2003) produced better estimates for BARK. The general models reported in this study showed the lowest Bias for FOLIAGE, but larger RMSE. Again, the model of White and Pritchett (1970) produced the largest underestimations on FOLIAGE.
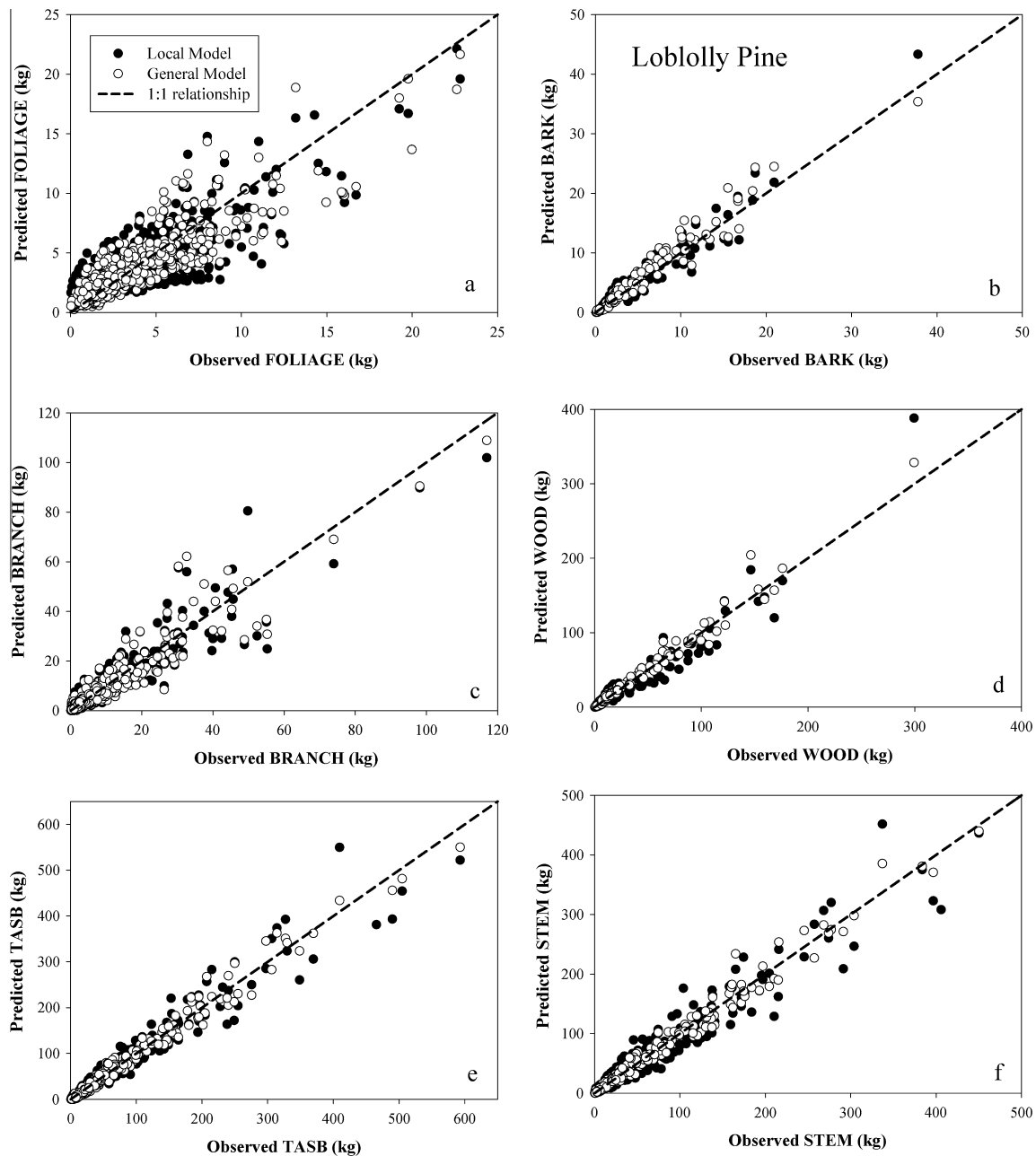
Fig. 4. Examples of evaluation of above-stump biomass models for loblolly pine. Observed versus predicted values using local model (filled circle, only uses dbh as explanatory variable) and general model (open circle, use dbh, H and stand parameters) for (a) FOLIAGE, (b) BARK, (c) BRANCH, (d) WOOD, (e) TASB and (f) STEM. Predicted BARK and WOOD were calculated using fitted models for STEM and BFRAC (BARK = BFRAC * STEM; WOOD = (1 − BFRAC) * STEM). Dashed line represents 1:1 relationship between observed and predicted values.

In the case of slash pine trees with a dbh smaller than 10 cm, TASB was better predicted by the models of Gholz and Fisher (1982), Jokela and Martin (2000) and Jenkins et al. (2003), while the local model T1 presented in this study produced Bias and RMSE slightly larger than those models (Table 12). The model of Swindel et al. (1979) for TASB produced the lowest Bias (−5.2%), but had a large RMSE (56.7%). In the case of FOLIAGE, the model of Gholz and Fisher (1982) showed the lowest Bias and RMSE, the model of Taras and Phillips (1978) showed the largest errors, and the general model F6 presented in this study showed intermediate results. The estimates of BRANCH from the general model B7 from this study had the lowest Bias and RMSE, while the model of Gholz and Fisher (1982) showed the largest estimation error. In the case

of WOOD, the model of Jenkins et al. (2003) showed the lowest Bias (5.6% underestimations), but had a large RMSE (7.04%), while the models of Pienaar et al. (1996) and Taras and Phillips (1978) showed the lowest RMSE (about 30%), but a larger Bias (about 20%). The estimates of WOOD from the present study (combining the models for BFRAC and STEM) showed intermediate prediction errors (Table 12). The estimates of BARK from the models reported in Jokela and Martin (2000) and Lohrey (1984) showed the smallest Bias (<4%) and the model of Taras and Phillips (1978) showed the lowest RMSE (25.4%). The estimates of BARK using the models reported in this study showed intermediate results for small trees. For STEM, the estimates using the models of Lohrey (1984) and Taras and Phillips (1978) showed the best agreement with
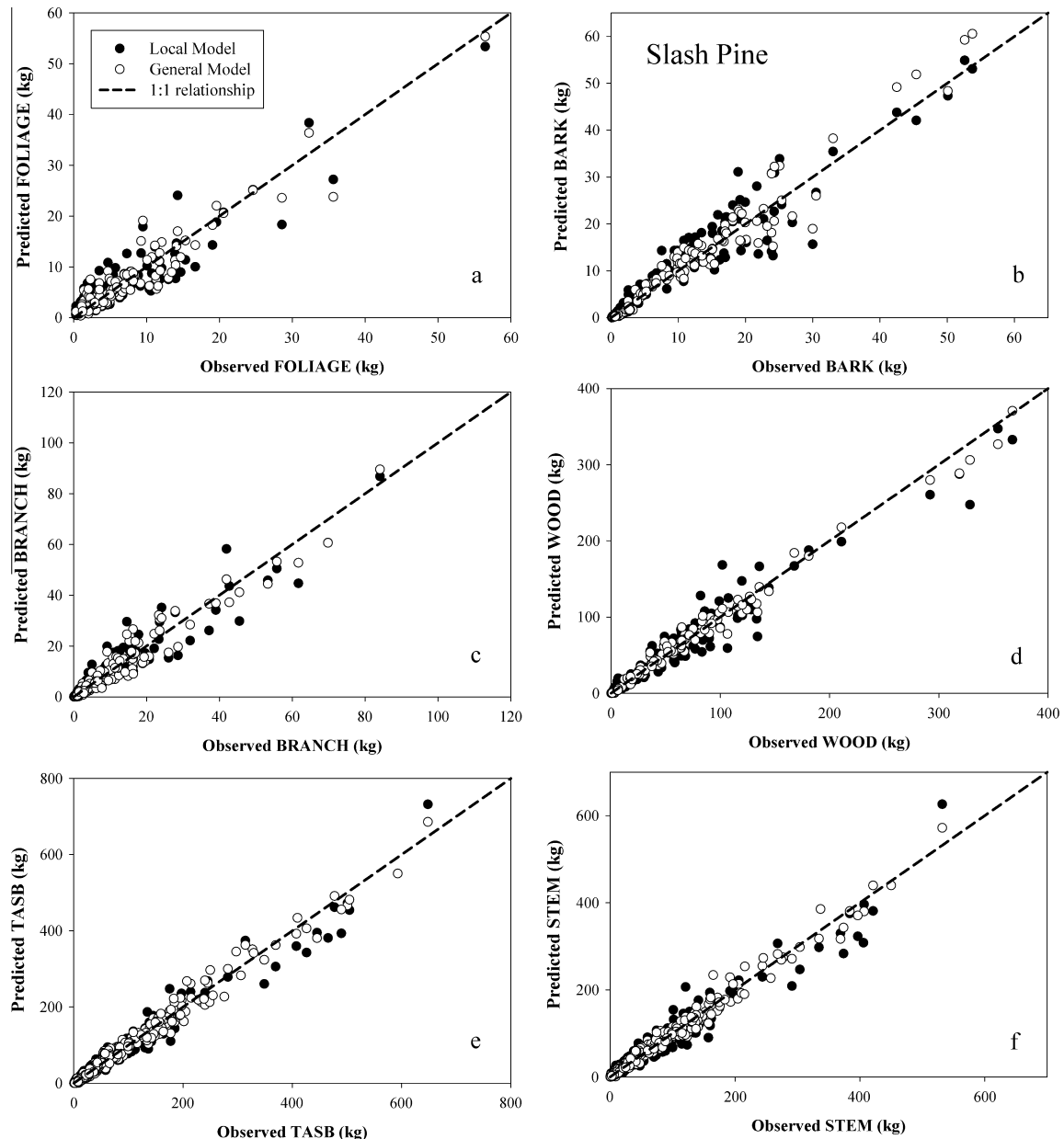
Fig. 5. Examples of evaluation of above-stump biomass models for slash pine. Observed versus predicted values using local model (filled circle, only uses dbh as explanatory variable) and general model (open circle, use dbh, H and stand parameters) for (a) FOLIAGE, (b) BARK, (c) BRANCH, (d) WOOD, (e) TASB and (f) STEM. Predicted BARK and WOOD were calculated using fitted models for STEM and BFRAC (BARK = BFRAC * STEM; WOOD = (1 − BFRAC) * STEM). Dashed line represents 1:1 relationship between observed and predicted values.

observed values. The model of Swindel et al. (1979) showed the largest estimation error and the models reported in this study for STEM, showed intermediate prediction errors (Table 12).

Similar to loblolly pine, the results for slash pine trees with a dbh between 10 and 20 cm produced the best predictions using the general models from this study, with the lowest Bias and RMSE for all above-stump biomass components analyzed. The model of White and Pritchett (1970) produced large errors in the estimations of FOLIAGE and BRANCH (305% and 135% underestimations, respectively; Table 12). For slash pine trees with a dbh larger than 20 cm, the models presented in this study produced the best prediction for all above-stump biomass components analyzed (Table 12). Only WOOD, estimated with the model of Pienaar et al. (1996), reported a slightly smaller Bias, but larger RMSE. Again, the model of White and Pritchett (1970) produced large underestimations of FOLIAGE and BRANCH.

4. Discussion

The set of prediction equations for above-stump biomass for loblolly and slash pine trees reported in this analysis provide useful tools for the study and management of these species. General and local models are presented to estimate all above-stump tree components. Users should decide which model to use depending on data availability and level of accuracy desired.

The new set of functions reported in this study were fit using trees growing over a large geographical area (Fig. 1), covering a wide range of ages and stand characteristics (Table 2), including the full range of stand-level productivity and biomass accumulation reported for both species (Table 3). For example, the sites with largest MAI$_W$ for both species (reported by Samuelson et al., 2008 and Jokela and Martin, 2000; for loblolly and slash pine, respectively) are included in our dataset. This comprehensive fitting

Table 10
Summary of model evaluation statistics using 10-fold cross validation for above-stump biomass estimations for loblolly and slash pine trees.

Species	Component	Model ID	Explanatory Variables	$\overline{O}$	$\overline{P}$	RMSE	Bias	R^2
Loblolly	BRANCH	B1[a]	dbh	6.28	6.23	4.48 (71.3)	0.05 (0.8)	0.815
		B2[a]	dbh, AGE	6.28	6.24	4.21 (67.1)	0.04 (0.7)	0.837
		B3[a]	dbh, AGE, N, BA	5.81	5.70	3.95 (68.0)	0.11 (1.9)	0.850
		B4[a]	dbh, H	6.28	6.23	4.48 (71.3)	0.05 (0.8)	0.815
		B5[a]	dbh, H, AGE	6.28	6.24	4.22 (67.2)	0.04 (0.6)	0.836
		B6[a]	dbh, H, AGE, N, BA	5.81	5.72	3.79 (65.2)	0.09 (1.5)	0.862
	FOLIAGE	F1[a]	dbh	3.47	3.46	1.71 (49.2)	0.01 (0.3)	0.710
		F2[a]	dbh, AGE	3.47	3.46	1.53 (44.1)	0.01 (0.3)	0.768
		F3[a]	dbh, AGE, N, Dp	3.38	3.40	1.49 (44.3)	−0.02 (−0.7)	0.775
		F4[a]	dbh, H	3.47	3.48	1.56 (45.1)	−0.01 (−0.3)	0.758
		F5[a]	dbh, H, AGE	3.47	3.49	1.46 (42.1)	−0.03 (−0.8)	0.788
		F6[a]	dbh, H, AGE, N, Dp	3.38	3.39	1.46 (43.3)	−0.02 (−0.5)	0.785
	STEM	S1	dbh	29.02	29.34	13.03 (44.9)	−0.31 (−1.1)	0.944
		S2	dbh, AGE	29.02	29.50	13.96 (48.1)	−0.48 (−1.6)	0.936
		S3	dbh, BA	26.83	27.36	12.20 (45.5)	−0.53 (−2.0)	0.948
		S4	dbh, H	29.02	28.52	8.03 (27.7)	0.5 (1.7)	0.979
		S5	dbh, H, AGE	29.02	28.44	7.26 (25.0)	0.59 (2.0)	0.983
		S6	dbh, H, AGE, N, Dp	26.83	26.82	6.63 (24.7)	0.01 (0.0)	0.985
	TASB	T1	dbh	38.70	37.76	14.34 (37.0)	0.95 (2.4)	0.955
		T2	dbh, AGE	AGE non-significant				
		T3	dbh, N, Dp	35.94	35.54	13.76 (38.3)	0.40 (1.1)	0.956
		T4	dbh, H	38.70	36.89	11.21 (29.0)	1.81 (4.7)	0.972
		T5	dbh, H, AGE	38.70	36.75	9.98 (25.8)	1.95 (5.0)	0.978
		T6	dbh, H, AGE, N, Dp	35.94	34.98	8.49 (23.6)	0.95 (2.7)	0.983
	BFRAC	BF1	dbh	0.174	0.175	0.0286 (16.4)	−0.00075 (−0.4)	0.714
		BF2	dbh, AGE	0.174	0.175	0.0274 (15.7)	−0.00037 (−0.2)	0.738
		BF3	dbh, Dq	0.174	0.175	0.0282 (16.2)	−0.00084 (−0.5)	0.723
		BF4	$dbh^2 \cdot H$	0.174	0.175	0.0259 (14.9)	−0.00063 (−0.4)	0.765
		BF5	$dbh^2 \cdot H$, AGE	0.174	0.175	0.0258 (14.8)	−0.00046 (−0.3)	0.768
		BF6	$dbh^2 \cdot H$, Dp	0.174	0.175	0.0257 (14.7)	−0.00062 (−0.4)	0.769
Slash	BRANCH	B1[a]	dbh	6.36	6.22	3.50 (55.0)	0.14 (2.2)	0.910
		B2[a]	dbh, AGE	6.36	6.25	2.84 (44.6)	0.10 (1.6)	0.930
		B3[a]	dbh, AGE, Dp	6.36	6.26	3.57 (56.1)	0.10 (1.6)	0.907
		B4[a]	dbh, H	6.36	6.42	3.16 (49.8)	0.19 (2.9)	0.927
		B5	dbh, H, AGE	6.36	6.19	2.83 (44.6)	0.17 (2.7)	0.941
		B6	dbh, H, AGE, Dp	6.36	6.12	2.86 (45.0)	0.24 (3.8)	0.940
	FOLIAGE	F1[a]	dbh	4.32	4.32	2.26 (52.3)	0.00 (0.1)	0.858
		F2[a]	dbh, AGE	4.32	4.36	2.24 (51.8)	−0.04 (0.9)	0.860
		F3[a]	dbh, AGE, N, Dp	4.32	4.25	2.18 (50.4)	0.07 (1.6)	0.868
		F4[a]	dbh, H	4.32	4.33	2.43 (56.3)	−0.01 (−0.2)	0.835
		F5	dbh, H, AGE	4.32	3.60	2.93 (67.9)	0.72 (16.6)	0.861
		F6[a]	dbh, H, AGE, N, Dp	4.32	4.32	2.06 (47.7)	−0.00 (−0.1)	0.882
	STEM	S1	dbh	38.59	38.92	15.78 (40.9)	−0.34 (−0.9)	0.954
		S2	dbh, AGE	38.59	39.80	12.53 (32.5)	−1.21 (−3.1)	0.971
		S3	dbh, AGE, N	38.59	39.50	12.86 (33.3)	−0.91 (−2.4)	0.969
		S4	dbh, H	38.59	37.61	10.1 (26.2)	0.98 (2.5)	0.981
		S5	dbh, H, AGE	38.59	38.17	9.43 (24.4)	0.42 (1.1)	0.983
		S6	dbh, H, AGE, N, Dp	38.59	38.08	8.09 (21.0)	0.5 (1.3)	0.988
	TASB	T1	dbh	49.42	48.83	14.74 (29.8)	0.59 (1.2)	0.972
		T2	dbh, AGE	49.42	49.42	13.22 (26.8)	−0.01 (0.0)	0.978
		T3	dbh, AGE, Dp	49.42	49.47	13.21 (26.7)	−0.06 (−0.1)	0.978
		T4	dbh, H	49.42	47.57	11.25 (22.8)	1.85 (3.7)	0.984
		T5	dbh, H, AGE	49.42	47.95	11.24 (22.7)	1.47 (3.0)	0.984
		T6	dbh, H, AGE, N, Dp	49.42	47.94	9.71 (19.6)	1.48 (3.0)	0.988
	BFRAC	BF1	dbh	0.237	0.238	0.0437 (18.5)	−0.00115 (−0.5)	0.746
		BF2	dbh, AGE	0.237	0.236	0.0365 (15.4)	0.00025 (0.1)	0.823
		BF3	dbh, AGE, N	0.237	0.237	0.036 (15.2)	0.00012 (0.1)	0.828
		BF4	$dbh^2 \cdot H$	0.237	0.238	0.0366 (15.4)	−0.00099 (−0.4)	0.823
		BF5	$dbh^2 \cdot H$, AGE	0.237	0.237	0.0335 (14.2)	−0.00027 (−0.1)	0.851
		BF6	$dbh^2 \cdot H$, Dq, Dp	0.237	0.237	0.0343 (14.5)	−0.00072 (−0.3)	0.844

dbh: diameter outside-bark at 1.37 m height (cm); H: total tree height (m); AGE: tree age (yrs.); N: trees per hectare (ha^{-1}); Dq: quadratic mean diameter (cm); Dp: ratio between dbh and Dq (cm cm^{-1}); BA: stand basal area (m^2 ha^{-1}); BRANCH: total living branch biomass (kg); FOLIAGE: total living needles biomass (kg); STEM: above-stump stem over bark biomass (kg); TASB: total above-stump biomass (kg); BFRAC: ratio of BARK to STEM (kg kg^{-1}); $\overline{O}$: mean observed value; $\overline{P}$: mean predicted value; RMSE: root of mean square error (same unit as observed value); Bias: mean absolute bias (observed-predicted; same unit as observed value); R^2: coefficient of determination. Values in parenthesis are percentage relative to observed mean.

[a] Includes second parameter for dbh (variable allometric ratio model).

provide us confidence that the functions are useable over a broad range of management and standing development conditions.

The functions derived in our study estimate above-stump biomass directly. However, the equations would be useful in a variety of ecological applications including estimating ecosystem C balance and other ecosystem attributes of interest. For example, forest floor and understory biomass can be estimated from FOLIAGE (and hence leaf area) determinations (Gonzalez-Benecke et al., 2012); foliage respiration can be better calculated also from improved FOLIAGE determinations; coarse root biomass can be

Table 11
Comparison of mean absolute bias (Bias) and root mean square error (RMSE) between two models reported in this study (Local, using only dbh, and General, using dbh, *H* and stand parameters) and several functions reported in scientific literature for loblolly pine.

dbh class	Source	n	TASB			FOLIAGE			BRANCH			WOOD[a]			BARK[a]			STEM		
			$\overline{O}$ (kg)	Bias(%)	RMSE (%)	$\overline{O}$ (kg)	Bias (%)	RMSE (%)	$\overline{O}$ (kg)	Bias (%)	RMSE (%)	$\overline{O}$ (kg)	Bias (%)	RMSE (%)	$\overline{O}$ (kg)	Bias (%)	RMSE (%)	$\overline{O}$ (kg)	Bias (%)	RMSE (%)
<10	Baldwin (1987)	425	6.7	29.2	43.1	2.0	26.4	62.1	1.5	29.9	63.7	2.3	41.9	48.7	0.6	2.7	40.4	3.2	30.5	38.4
	Jenkins et al. (2003)	425		27.2	40.2		73.4	94.6		13.2	60.2		4.7	49.4		24.2	43.2		4.6	48.6
	Jokela and Martin (2000)	425		20.8	39.5		68.5	88.6		41.1	70.5		−16.1	67.5		−7.6	43.2		−18.9	63.5
	Naidu et al. (1998)	425		22.4	38.8		41.8	68.4		48.6	76.3		n.a.	n.a.		n.a.	n.a.		16.8	48.8
	Pienaar et al. (1987)	425		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		52.4	62.1		n.a.	n.a.		n.a.	n.a.
	Taras and Clark (1975)	425		46.7	57.2		86.5	107.1		79.3	107.8		7.7	35.0		−12.0	44.0		3.6	31.7
	Van Lear et al. (1984)	425		2.8	45.4		91.7	111.6		74.1	99.4		−97.1	172.2		−58.2	96.3		−92.5	151.2
	White and Pritchett (1970)	425		40.5	53.3		57.8	85.3		55.9	87.2		24.4	33.0		27.7	41.3		22.6	31.8
	Local Model[b]	425		34.7	45.8		35.7	64.7		45.4	73.4		9.1	51.1		5.5	40.1		4.0	50.6
	General Model[c]	425		26.9	40.3		25.5	51.9		25.2	70.1		14.7	32.4		7.3	32		8.8	33.3
10–20	Baldwin (1987)	251	46.3	−5.7	15.9	4.2	−51.7	69.1	7.8	−1.2	40.2	29.9	4.0	13.2	4.5	−42.1	52.7	34.2	−1.0	15.4
	Jenkins et al. (2003)	251		10.5	28.0		30.4	55.7		−9.2	40.8		22.2	49.6		3.6	28		12.6	38.5
	Jokela and Martin (2000)	251		−16.2	28.0		−1.3	48.9		−23.9	48.5		−6.1	33.1		−5.7	28.7		−15.8	36.1
	Naidu et al. (1998)	251		−5.4	23.3		−29.5	57.0		20.2	46.1		n.a.	n.a.		n.a.	n.a.		12.0	36.5
	Pienaar et al. (1987)	251		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		6.9	14.2		n.a.	n.a.		n.a.	n.a.
	Taras and Clark (1975)	251		−7.3	21.3		35.3	66.0		33.5	58.9		−19.9	25.9		−52.1	64		−23.6	31.4
	Van Lear et al. (1984)	251		−42.3	50.9		60.4	76.6		26	47.1		−59.6	68.1		−43.8	52.3		−71.3	82
	White and Pritchett (1970)	251		6.6	19		−109.2	161.2		18.5	51.9		14.7	26.4		26.1	37.5		18.0	26.8
	Local Model[b]	251		−4.0	22.7		−13.8	48.8		0.5	39.2		4.6	33.9		−9.1	28.8		−6.6	33.0
	General Model[c]	224		−1.9	16.3		−10.8	35.4		4.1	38.5		−4.6	14.8		−13.5	26.4		−3.7	16.9
>20	Baldwin (1987)	68	202.9	−1.1	14.8	9.7	−46.0	59.9	29.0	5.4	40.4	134.6	−4.9	21.8	16.8	−36.1	41.5	164.1	0.4	13.8
	Jenkins et al. (2003)	68		28.8	37.2		7.4	29.5		10.3	39.1		33.6	37.5		2.4	15.5		33.3	42.5
	Jokela and Martin (2000)	68		−4.6	19.7		−29.7	41.4		−42.5	62.7		−3.7	21.8		7.0	15.5		2.0	21.0
	Naidu et al. (1998)	68		10.1	22.0		−30.4	41.9		25.7	46.2		n.a.	n.a.		n.a.	n.a.		22.0	31.2
	Pienaar et al. (1987)	68		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		−11.4	39.9		n.a.	n.a.		n.a.	n.a.
	Taras and Clark (1975)	68		−9.9	18.5		−1.8	30.8		7.4	40.4		−21.9	33.5		−44.1	49.8		−14.5	21.5
	Van Lear et al. (1984)	68		−27.9	36.1		33.6	44.7		−5.8	42.5		−43.2	54.8		−20.2	25.9		−34.6	42.4
	White and Pritchett (1970)	68		17.4	23.7		−242.6	266.1		17.8	42.3		24.4	28.6		38.9	44		32.6	38.9
	Local Model[b]	68		0.9	19.2		0.7	33		−3.6	37.8		−1.4	23.5		−7.1	18.6		2.3	21.3
	General Model[c]	59		0.8	10.9		0.5	36.5		−2.9	34.3		−5.1	15.1		−9.2	19.5		1.7	10.9

dbh: diameter outside-bark at 1.37 m height (cm); *n*: number of observations; $\overline{O}$: observed mean (kg); Bias: mean absolute bias (observed-predicted; %); RMSE: root mean square error (%); TASB: total above-stump biomass; FOLIAGE: total living needles biomass; BRANCH: total living branch biomass; WOOD: above stump stem wood inside bark biomass; BARK: above stump stem bark biomass; STEM: above stump stem over bark biomass.
[a] WOOD and BARK were calculated using the models for STEM and BFRAC.
[b] Local models for TASB, FOLIAGE, BRANCH, BFRAC and STEM corresponds to models T1, F1, B1, BF1 and S1, respectively.
[c] General models for TASB, FOLIAGE, BRANCH, BFRAC and STEM corresponds to models T6, F6, B6, BF6 and S6, respectively.

Table 12

Comparison of mean absolute bias (Bias) and root mean square error (RMSE) between two models reported in this study (Local, using only dbh, and General, using dbh, H and stand parameters) and several functions reported in the scientific literature for slash pine.

dbh class	Source	n	TASB $\bar{O}$ (kg)	TASB Bias (%)	TASB RMSE (%)	FOLIAGE $\bar{O}$ (kg)	FOLIAGE Bias (%)	FOLIAGE RMSE (%)	BRANCH $\bar{O}$ (kg)	BRANCH Bias (%)	BRANCH RMSE (%)	WOOD[a] $\bar{O}$ (kg)	WOOD[a] Bias (%)	WOOD[a] RMSE (%)	BARK[a] $\bar{O}$ (kg)	BARK[a] Bias (%)	BARK[a] RMSE (%)	STEM $\bar{O}$ (kg)	STEM Bias (%)	STEM RMSE (%)
<10	Gholz and Fisher (1982)	153	4.9	12.2	42.5	1.6	35.7	56.3	0.7	83.2	107.0	1.7	−23.0	101.9	0.8	−7.2	53.2	2.6	−22.0	83.7
	Jenkins et al. (2003)	153		23.1	39.7		71.9	86.3		−52.6	105.7		−5.6	70.4		56.7	75.2		11.2	51.0
	Jokela and Martin (2000)	153		11.3	43.4		77.1	89.2		51.8	70.3		−60.6	122.8		−3.9	36.1		−47.8	91.9
	Lohrey (1984)	153		38.0	46.2		57.0	69.3		39.9	68.1		38.1	46.6		2.5	37.5		24.8	31.9
	Pienaar et al. (1996)	153		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		20.3	29.9		n.a.	n.a.		n.a.	n.a.
	Swindel et al. (1979)	153		−5.2	56.7		81.2	93.7		62.0	80.2		n.a.	n.a.		n.a.	n.a.		−79.8	142.0
	Taras and Phillips (1978)	153		57.4	64.8		87.4	101.6		82.8	104.8		20.0	31.5		15.5	25.4		25.0	31.4
	White and Pritchett (1970)	153		36.3	52.1		67.3	100.3		−15.3	90.8		24.7	36.1		41.6	53.6		29.3	38.2
	Local Model[b]	153		20.3	44.5		78.5	90.8		38.1	61.8		−16.9	90.1		−10.0	45.1		−19.0	72.9
	General Model[c]	153		51.6	60.1		73.7	84.7		34.3	64.4		41.5	52.4		41.3	57.6		39.4	50.2
10–20	Gholz and Fisher (1982)	73	71.0	−11.6	26.6	5.2	14.9	54.0	8.4	65.5	83.4	47.6	−22.4	42.3	10.7	−35.2	53.7	57.7	−24.8	43.5
	Jenkins et al. (2003)	73		33.9	45.2		37.4	62.8		−13.4	43.2		38.9	53.8		49.5	64.3		40.8	55.1
	Jokela and Martin (2000)	73		9.1	25.3		−12.5	49.3		−7.9	36.9		13.4	35.2		17.4	41.5		14.0	35.3
	Lohrey (1984)	73		−0.6	16.8		12.3	42.6		30.9	51.8		2.3	20.9		−43.0	58.1		−6.0	22.2
	Pienaar et al. (1996)	73		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		−6.7	20.0		n.a.	n.a.		n.a.	n.a.
	Swindel et al. (1979)	73		−9.5	24.4		19.3	51.3		31.2	52.9		n.a.	n.a.		n.a.	n.a.		−20.5	37.6
	Taras and Phillips (1978)	73		1.1	15.4		20.9	58.3		27.5	54.0		−8.6	23.4		−14.1	31.7		−10.7	23.8
	White and Pritchett (1970)	73		−36.6	43.4		−305.8	365.5		−135.3	154.0		−1.0	19.9		19.7	36.8		2.8	19.4
	Local Model[b]	73		2.2	22.7		9.7	48.1		4.0	38.6		3.4	31.6		−3.7	36.4		2.0	31.1
	General Model[c]	73		0.3	15.0		9.9	40.4		11.0	33.6		−2.2	17.8		1.2	24.5		−1.5	15.7
>20	Gholz and Fisher (1982)	26	227.9	−30.3	35.8	11.2	31	49.4	26.4	45.7	57.9	163.3	−41.3	49.1	27.0	−63.5	70.2	190.3	−44.4	51.9
	Jenkins et al. (2003)	26		42.2	52.2		26.6	43.3		9.1	38.5		48.5	60.4		42.9	49.4		47.7	58.7
	Jokela and Martin (2000)	26		13.8	23.7		−63.1	79.4		−44.3	58.5		25.9	38.3		19.2	28.7		24.9	36.7
	Lohrey (1984)	26		−2.2	11.2		−21.8	41.8		14.9	31.9		4.2	14.2		−49.5	53		−3.4	13.1
	Pienaar et al. (1996)	26		n.a.	n.a.		n.a.	n.a.		n.a.	n.a.		1.8	13.0		n.a.	n.a.		n.a.	n.a.
	Swindel et al. (1979)	26		−4.7	15.1		−9.8	36.3		17.4	36.6		n.a.	n.a.		n.a.	n.a.		−11.4	20.7
	Taras and Phillips (1978)	26		−0.3	11.1		1.2	36.7		9.3	37.3		−4.6	13.1		−12.0	18.6		−8.4	14.2
	White and Pritchett (1970)	26		−27.2	29.4		−398.2	434.8		−178.3	199.2		14.7	25.6		21.1	29.1		15.6	25.8
	Local Model[b]	26		−1.1	13.4		−21.4	42.1		−7.0	30.8		1.5	18.0		−9.5	18.5		−0.1	17.2
	General Model[c]	26		−0.3	7.2		−19.2	35.1		−6.3	19.7		2.7	7.3		−8.2	16.4		1.1	6.9

dbh: diameter outside-bark at 1.37 m height (cm); n: number of observations; $\bar{O}$: observed mean (kg); Bias: mean absolute bias (observed-predicted;%); RMSE: root mean square error (%); TASB: total above-stump biomass; FOLIAGE: total living needles biomass; BRANCH: total living branch biomass; WOOD: above stump stemwood inside bark biomass; BARK: above stump stembark biomass; STEM: above stump stem over bark biomass.

[a] WOOD and BARK were calculated using the models for STEM and BFRAC.
[b] Local models for TASB, FOLIAGE, BRANCH, BFRAC and STEM corresponds to models T1, F1, B1, BF1 and S1, respectively.
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estimated using STEM to coarse root ratios (Johnson, 1990; Albaugh et al., 2006; Gonzalez-Benecke et al., 2014b); or fine root biomass can be calculated using FOLIAGE to fine root ratios (King et al., 1999; Adegbidi et al., 2004). Many forest ecologists have used allometric equations based on biomass equations such as ours to help describe and understand processes such as nutrient dynamics, carbon sequestration, growth and competition in forest ecosystems (Gholz et al., 1985, 1991; Clark et al., 2001; Ducey and Allen, 2001; Sampson et al., 2001; Martin and Jokela, 2004; Albaugh et al., 2008; Gonzalez-Benecke et al., 2010, 2011). Our new biomass equations should improve these types of analyses and syntheses in loblolly and slash pine forest ecosystems. Biological process models which incorporate allometry-based rules for allocation (e.g. 3-PG; Landsberg and Waring, 1997) also will benefit from these more robust and flexible functions. Models and modeling systems incorporating these equations can in turn then be used to explore the implications of varying tree-level allometry on stand structure and stand dynamics.

Figs. 2 and 3 reveal some similarities and differences in the relationship between dbh and components of above-stump biomass between species. For example, the relationship between dbh and FOLIAGE and BRANCH were similar for both species, although the values for loblolly pine were more variable around their predictions. On the other hand, the relationship between dbh and TASB, STEM and BFRAC differed between the species. For the same dbh, slash pine tended to have larger stem and bark biomass accumulation, and therefore TASB. This is likely an effect of both larger juvenile stem wood density (Clark and Schmidtling, 1989) and thicker bark (Hare, 1965) in slash pine. As the scope of this study was to generate specific biomass equations for each species, we did not test species differences in the allometric relationships evaluated.

Due to the high labor intensity required for destructive sampling of tree biomass, allometric functions are usually developed from a limited number of trees. Zianis et al. (2005), in an extensive review of biomass equations in Europe, found that 75% of the studies had sampled less than 50 trees. The outcomes of those functions are also commonly restricted to the geographic location and the specific characteristics of development and productivity of the stand where that sampling was carried out (Weiskittel et al., 2011). When biomass estimation is needed for stands located outside the range of age, productivity or geographic distribution associated with the original sampling, the reliability of those estimates may be questioned, as biomass predictions can have large discrepancies depending on the function being applied (Parresol, 1999). Van Lear et al. (1986) pointed out that discrepancies in biomass predictions between the different equations can result from changes in growth partitioning and/or tree taper variation associated with stand productivity and development.

A number publications have presented generalized allometric regressions for different tree species (Schmitt and Grigal, 1981; Pastor et al., 1984; Ben Brahim et al., 2000; Jenkins et al., 2003; Chave et al., 2005; Pilli et al., 2006; Zhang and Kondragunta, 2006; António et al., 2007; Zeng and Tang, 2011), but most of those studies reported equations that only relied on dbh as a predictor; some used dbh and H and only a few used dbh, H and AGE in their regional equations. Other authors have used crown length/area or sapwood area in order to improve estimates, mainly for crown components (Ritson and Sochaki, 2003; Pitt and Bell, 2004; António et al., 2007; Williams and Gresham, 2006; Samuelson et al., 2008) or wood density (Brown, 1997; Ketterings et al., 2001; Basuki et al., 2009), but those attributes are not easily available in regular inventories or with most growth and yield models. The equations presented here allow robust estimates of biomass components using easily available stand attributes as covariates.

Several authors have published biomass functions for loblolly and slash pine trees that were based on dbh as a single predictor

variable (Swindel et al., 1979; Gholz and Fisher, 1982; Pehl et al., 1984; Van Lear et al., 1984; Naidu et al., 1998; Jokela and Martin, 2000; Adegbidi et al., 2002; Jenkins et al., 2003; Samuelson et al., 2004; Coyle et al., 2008), while other authors have reported functions using as predictors both dbh and H (White and Pritchett, 1970; Taras and Clark, 1975; Taras and Phillips, 1978; Gibson et al., 1985; Lohrey, 1984; Baldwin 1987; Tew et al., 1986; Jokela et al., 1989; Amateis et al., 1992; Albaugh et al., 1998; Rubilar et al., 2005; Williams and Gresham, 2006; Roth et al., 2007). For these species, only a few reports have included AGE as a covariate (Baldwin, 1987; Albaugh et al., 1998) and none has included other stand attributes such as BA, N or Dq. In their study comparing biomass equations for sawtimber sized loblolly pine, Van Lear et al. (1984) concluded that regional equations based on dbh may introduce large errors in biomass estimations, due to differences in partitioning associated with tree taper variations; the inclusion of H as predictor should improve the predictions.

The use of the variable allometric ratio model resulted in significant improvement in the estimation of FOLIAGE and BRANCH. Similar to the results of Ruark et al. (1987), this model did not improve estimates of TASB and STEM. In the absence of other stand attributes, the large reduction in Bias for FOLIAGE and BRANCH estimations argues for the use of this model when assessments of crown component biomass are required.

For both species, including all the tree components evaluated, the inclusion of H significantly improved the estimates. Similar responses have been documented elsewhere with other species, e.g. Quercus suber L. (Parresol, 1999), Eucalyptus spp. (Bi et al., 2004), Picea glauca (Moench) Voss (Pitt and Bell, 2004), and Eucalyptus globulus Labill. (António et al., 2007). In many cases, H is not available and estimations of tree biomass are restricted to functions that rely only on dbh as a predictor. In those cases, stand variables that can account for tree taper or stand development stage could be used as surrogates for H. Several authors have used stand attributes as covariates for increasing the accuracy of the estimations of H (Larsen and Hann, 1987; Huang and Titus, 1994; Staudhammer and LeMay, 2000; Leduc and Goelz, 2010; Gonzalez-Benecke et al., 2014a) or stem volume (Harrison and Borders, 1996; Pienaar et al., 1996; Gonzalez-Benecke et al., 2014a). Hence, if H and stem volume can be better estimated from known stand attributes, then tree biomass predictions should improve when stand attributes that account for stand development, competition and productivity are included as covariates. In their study comparing biomass functions for Picea mariana (Mill.), Grigal and Kernik (1984) concluded that stand conditions affect crown and stem morphology and hence the allometry of individual trees.

When comparing biomass and nutrient content equations for successive rotations of loblolly pine stands, Rubilar et al. (2005) reported that, with the exception of WOOD, equation parameter estimates for all above-stump biomass components were different between rotations. The authors concluded that rotation-specific equations were needed for each biomass component. We agree with the authors, but instead of using separate equations for each rotation, we suggest that the inclusion of the stand variables that account for differences in productivity and tapering could be used instead.

The effects of silvicultural treatments (modifying competition and resource availability) on biomass allometry are not consistent in the literature and therefore are often confounded by ontogenetic effects. When evaluating the effects of cultural practices intensity and planting density on the above-ground allocation of 12-year old loblolly pine trees, Subedi et al. (2012) pointed out that planting density affected the allocation of all above-ground components, while cultural intensity only affected foliage and dead branch allocation. Jokela and Martin (2000) reported an interesting

effect of ontogeny and stand development on above-stump allom-etry for loblolly and slash pine trees. At four years of age they found differences in allometry between untreated plots and those treated with sustained fertilization and weed control, and at 13 years of age they did not find differences in allometry due to treatments. Also at age four, Coyle et al. (2008) reported the effect of fertilization and irrigation on allometry of loblolly pine trees. King et al. (1999) reported slight changes in allometry in response to altered resource availability (due to sustained fertilization and irrigation) with loblolly pine, and argued that those changes were greatly affected by ontogenetic development of the trees. In a fer-tilization x genetics study, Retzlaff et al. (2001) reported no changes in tree allometry due to treatments in 5-year-old loblolly pine trees. Samuelson et al. (2004, 2008) reported no effects of fer-tilization and irrigation on the relationship between tree size and the biomass of different components of loblolly pine trees, but they fitted different models for trees of different ages (2–10 years old). In a 25-year-old slash pine stand, Jokela et al. (1989) reported that early fertilization affected foliage and branch wood allometry, but not stem wood allometry. In all these examples, the responses to silvicultural treatments, such as irrigation, weed control and fertil-ization, were associated with changes in BA and SI. Following the same rationale in southern pine growth and yield simulation, the effects of silvicultural treatments have been commonly associated with changes in BA and SI (Harrison and Borders, 1996; Pienaar et al., 1996; Hynynen et al., 1998; Amateis et al., 2000). The most widely used index of stand productivity, SI, was not included in our models because it was not available for most of the data col-lected. In our dataset, the inclusion of other attributes such as BA and Dq, in combination with AGE will effectively substitute for SI, and account for much of the variation in inherent stand produc-tivity. Even though SI was available only in 30% of the dataset, we tested the effect of SI as a covariate. Site index provided little improvement in model fitting when other stand attributes were included in the model. For example, for TAGB the model performed slightly better only for loblolly pine, increasing R^2 by less than 0.0033. For slash pine, SI was non-significant. A similar response was observed for all other biomass components.

When AGE was included with dbh, it resulted in a significant improvement of predictions for all biomass components for slash pine, but not for STEM and TASB on loblolly pine trees. This response suggests that the effects of ontogeny on tree growth differ between species, as was pointed out by Jokela and Martin (2000). When AGE was included in the model that also used dbh and H, it was significant in all components for both species. In general, AGE produced large improvement in prediction ability when both dbh and H were included in the models. This response may be related to the changes in stem form and the H-dbh relationship as trees grow and age. Other authors have recognized the effects of AGE in biomass allometry for these species. For example, Jokela and Martin (2000), Adegbidi et al. (2002) and Samuelson et al. (2004, 2008), fitted different models as stands aged, while Harrison and Borders (1996) and Pienaar et al. (1996) fitted general models for STEM for loblolly and slash pine, respectively, but included AGE as a covariate, in addition to dbh and H. AGE has been also recognized as a supplementary variable in allometric func-tions for other tree species such as *Pinus pinaster* Aiton (Porté et al., 2002; Shaiek et al., 2011), *Metasequoia glyptostroboides* Hu and W.C. Cheng (Williams et al., 2003); *Eucalyptus* hybrids (Saint-André et al., 2005), and *Fagus sylvatica* L. (Genet et al., 2011).

Seasonal dynamics of FOLIAGE (and therefore LAI) of loblolly and slash pine has been described elsewhere (Dalla-Tea and Jokela, 1991; Gholz et al., 1991; Dougherty et al., 1995; Zhang et al., 1997). Within a growing season, on a specific site, FOLIAGE can vary up to 100% depending on stand and environmental condi-tions. Generally, minimum foliage amounts occur in

February–March, while August–September represents peak peri-ods of foliage accumulation (Dalla-Tea and Jokela, 1991; Dougherty et al., 1995). Our models for FOLIAGE are based on observations where sampling date was not available and, there-fore, not considered in model fitting. Our models for estimating crown component biomass (FOLIAGE and BRANCH) suggest that, for the same size and stand conditions, older trees had less living crown biomass than younger trees. This result is in general agree-ment with several studies that have reported a decline in southern pine foliage production as trees age (Gholz and Fisher, 1982; Allen et al., 1990; Long and Smith, 1992; Martin and Jokela, 2004). In older southern pine stands, nutrient deficiencies, especially nitro-gen and phosphorus, may develop (Gholz et al., 1985; Piatek and Allen, 1999; Martin and Jokela, 2004) and contribute to foliage declines because of increased stand nutrient demands and lower soil nutrient supply due to immobilization in the forest floor and plant biomass (trees and understory) (Piatek and Allen, 2001; Ducey and Allen, 2001). Additionally, temporal declines in foliage biomass in southern pines could be related to density related crown recession (especially in unthinned stands), needed to pro-vide structural stability (Landsberg and Sands, 2011) and an increased propensity for water deficits resulting from reductions in hydraulic conductivity (Ryan et al., 2006). It should be noted, however, that the equations reported for crown components would not generally have sufficient sensitivity to accurately predict changes in foliage biomass resulting from nutrient ameliorative treatments and natural seasonal dynamics.

The parameters associated with Dp were significant in most cases, indicating that the level of dominance of trees within the stand was an attribute that should be considered in forest biomass assessments. Other authors have fitted different models for sup-pressed or dominant trees for loblolly pine (Naidu et al., 1998) or for slash pine (Gholz and Fisher, 1982). In our study, when Dp was significant the sign of the parameter estimate was always positive. This implies that dominant trees with the same size and AGE in the stand would accumulate more biomass than trees with a lower level of dominance.

Stand characteristics used as covariates, in addition to AGE, resulted in significant improvements in model fitting and predic-tion ability for all tree components, especially when H was unknown. When AGE and H were known, there were moderate improvements due to the inclusion of stand variables in the predic-tion of stem components. Few authors have reported the effects of stand and site factors on tree allometry. However, Crow (1978), Alemdag and Stiell (1982) and Russell et al. (2009) found a signif-icant effect of stand density on model performance. A different response was reported by António et al. (2007), who showed a sig-nificant effect of dominant height and a slight effect of stand den-sity on tree allometry for *E. globulus*. They concluded that the addition of H and AGE may have compensated for the effects of competition and site quality. In our dataset, the improvements in model performance were larger for crown components than for stem components. These results imply that stand variables can be used as surrogates of H, accounting for changes in the taper and allometry of the trees growing under different stand conditions.

When compared with some reported equations for both species, our general model that included dbh, H, AGE and stand variables performed better than the tested functions for trees with a dbh lar-ger than 10 cm. Nevertheless, for trees with a dbh smaller than 10 cm, the models presented in this study showed an intermediate performance when compared with other published models. These results suggest a trade-off in the precision and accuracy of our models: for small trees (young stands) site-specific equations may be preferred to our models. It is important to recall that, for trees with dbh smaller than 10 cm, for both species the average

TASB was about 5 kg, and the magnitude of the errors at that size class were negligible compared with the gains in model prediction for larger trees.

5. Conclusion

The equations presented in this study are a robust alternative to previous biomass prediction models reported for loblolly and slash pine. We recommend using the equations obtained in this study within the range of data used to fit the models (see Table 2). These sets of equations provide a valuable alternative to available models and are intended as a tool to support present and future management decisions for the species, allowing regional assessments of stand biomass and a variety of other ecological applications including estimating ecosystem C balance and other ecosystem attributes of interest, across a wide range of ages, sizes and stand conditions. Incorporation of these functions into stand-level productivity models should improve the flexibility and robustness of biomass predictions from those models, and can also serve as a means to explore the stand-level implications of tree-level variation in allometry.

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