SPECIES-SPECIFIC BIOMASS EQUATIONS FOR SMALL-SIZE TREE SPECIES IN SECONDARY TROPICAL FORESTS†

[ECUACIONES ESPECÍFICAS DE BIOMASA PARA ÁRBOLES DE DIÁMETRO-PEQUEÑO EN BOSQUES TROPICALES SECUNDARIOS]

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SUMMARY

Secondary tropical forests are largely dominated by small-diameter trees. Their contribution to the total stand productivity may be determinant for ecosystem functioning. However, the biomass contained in small-size trees is frequently ignored because they are rarely included in forest inventories, as well as due to the lack of biomass equations for such trees. The aim of this study was to generate specific biomass equations by tree structural components and total-tree biomass for 22 species (diameter at breast height-DBH ≤ 10 cm diameter) structurally important of secondary tropical forests in southeast Yucatán peninsula. The biomass equations were generated using two fitting approaches. First, using the additive approach where the biomass equations by structural tree components (stem, branches and foliage) were simultaneously fitted. Second, the tree-level approach where the total-tree biomass was independently fitted. We used DBH, total height (TH) and wood density (WD) as predictor variables during the fitting process. The performance of each total-tree biomass equation was compared to generalized biomass equations developed in other tropical forests. The variance explained of observed biomass across tree species were stem, 64% to 99%; branch, 24% to 95%; foliage, 35% to 94% for equations by structural tree components; while the explained variance for total tree biomass equations was between 94 to 99 %. The inclusion of TH and WD as predictor variables in the equation structure, significantly improved the goodness of fit statistics. These are the first equations developed for small-size tree species in secondary forests of Yucatán peninsula. We observed that generalized equations developed for other tropical forests, in some cases overestimated up to ~ 44.2% and in other cases underestimated up to ~ 48.4% the mean total-tree biomass. When we applied our equations to forest inventory data, they showed a better predicting performance than generalized equations. Therefore, they are reliable for estimating biomass of small-size tree species in similar forest types. Our equations could be used for biomass-carbon estimation in tropical secondary forests composed by high densities of small-size tree species; therefore, they are relevant within climate change contexts.

Keywords: Allometric equations; biomass stocks; additive system equations; simultaneous fitting; non-linear models; wood density.

RESUMEN

Los bosques tropicales secundarios generalmente están dominados en gran parte por árboles de diámetros-pequeños. Su contribución a la productividad total puede ser relevante para el funcionamiento de los ecosistemas. Sin embargo, la biomasa contenida en los árboles-pequeños frecuentemente es ignorada debido a que rara vez son incluidos en los inventarios forestales, así como y por la falta de ecuaciones de biomasa para ellos. El objetivo de este estudio fue generar ecuaciones-específicas de biomasa por componente estructural del árbol y biomasa total-árbol para 22 especies (diámetro normal-DBH ≤ 10 cm) estructuralmente importantes de los bosques secundarios dl sureste de la Península de Yucatán. Las ecuaciones de biomasa se generaron usando dos enfoques de ajuste. Primero, usando el enfoque aditivo se ajustaron simultáneamente las ecuaciones de biomasa por componente estructural del árbol; fuste, ramas y

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follaje. Segundo, con el enfoque a nivel árbol se ajustó de manera independiente la biomasa total árbol. En el proceso de ajuste se utilizó el DBH, la altura total del árbol (TH) y la densidad de la madera como variables independientes. El desempeño de cada ecuación de biomasa total-árbol se comparó contra aquel de ecuaciones de biomasa generalizadas desarrolladas para otras regiones tropicales. La varianza de la biomasa observada explicada por las ecuaciones aditivas para las especies incluidas en este estudio fue: fuste, 64% a 99%; ramas, 24% a 95%; follaje, 35% hasta 94%; mientras que la varianza explicada de la ecuación de biomasa total fue entre 94 a 99%. La inclusión de TH y WD como variables independientes en la estructura de las ecuaciones, mejoraron significativamente los estadísticos de bondad de ajuste. Estas ecuaciones son las primeras que se desarrollan para especies de diámetros-pequeños en bosques secundarios de la península de Yucatán. Las ecuaciones generalizadas desarrolladas para otros bosques tropicales sobreestimaron en algunos casos hasta ~ 44.2% y en otros casos subestimaron ~ 48.4% de la biomasa total promedio por árbol. Cuando aplicamos las ecuaciones a datos de inventario, estas presentaron una capacidad predictiva mejor que las ecuaciones generalizadas. Por tanto, las ecuaciones ajustadas son confiables para estimar la biomasa de tipos de bosques similares. Las ecuaciones desarrolladas pueden ser utilizadas para estimar la biomasa ycarbono de bosques tropicales secundarios compuestos por una alta densidad de especies con diámetros pequeños; por tanto, consideramos que son relevante en el contexto de cambio climático.

Palabras clave: Ecuaciones alométricas; existencias de biomasa; sistema de ecuaciones aditivas; ajuste simultáneo; modelos no-lineales; densidad de la madera.

INTRODUCTION

The interest of secondary tropical forests is increasing, not only for its extension or its role in biodiversity conservation, but also for its high resilience in biomass recovering from anthropogenic and natural disturbances (Chazdon *et al.*, 2010; Memiaghe *et al.*, 2016; Poorter *et al.*, 2016). Very often, the biomass estimation in tropical forests have been based only with data of large trees (> 10 cm DBH) leaving small-size trees (DBH < 10 cm) unaccounted, since the common assumption is that small-size tree biomass is less than 5% of large-size tree biomass (Lugo and Brown, 1992; Chave *et al.*, 2003; Vincent *et al.*, 2015). However, this assumption may not be applicable for all tropical forests because they are highly dynamic and their structure re the result of different factors (Vincent *et al.*, 2015; Chazdon, 2003; Poorter *et al.*, 2016). For instance, land use change leads to heterogeneous landscapes and canopy variations dominated by secondary forests that contain greater number of small-size trees(here denoted as trees 1 cm ≤ DBH ≤ 10 cm) (Chave *et al.*, 2003; Dupuy *et al.*, 2012a; Memiaghe *et al.*, 2016). Small-size trees are important component of the diversity of woody plants of secondary tropical forests and they can contribute significantly to the total stand biomass (Dupuy *et al.*, 2012a; Memiaghe *et al.*, 2016).

The secondary forests of the Yucatan peninsula in Mexico are dominated for small-size tress. In absolute values, the density of individuals > 5 cm DBH in forests of Campeche range from 1 000 to 3 422 trees per hectare in stands of 5 to 20 years-old, and if individuals > 2 DBH are included, the tree density may reach up to 4 000 trees per hectare (Schmook, 2010; Román-Dañobeytia *et al.*, 2014). In relative values, the contribution of small-trees to the total density per unit area, has been reported in the order of 2.4% to 60% (Zamora *et al.*, 2008; Gutiérrez-Báez *et al.*, 2013). In other secondary tropical forests, for example in China, Kenia, Papua New Guinea, Costa Rica, and Panamá, small trees can reach 25% to 93.6% of the total tree density (Chave *et al.*, 2003; Brandeis *et al.*, 2006; Kuyah *et al.*, 2012; Vincent *et al.*, 2015; Memiaghe *et al.*, 2016; He *et al.*, 2018). Regarding tree biomass, small trees contribute between 3.6% up to 35.05% depending on the forest successional stage (Alief, 2012; Kuyah *et al.*, 2012; Lima *et al.*, 2012; Memiaghe *et al.*, 2016). These observations are consistent with the idea that small-size trees can show a high variation in their contribution to the overall biomass.

The accurate biomass estimation of tropical forests depends on the quality of the allometric equations for structural tree components such as stem, branch and foliage, and total-tree biomass (Chave *et al.*, 2005; Dong *et al.*, 2014). Methods for estimating tree biomass could be classified into allometric equations at tree-level, structural component-level, and additive biomass equations (Parresol, 2001; Sanquetta *et al.*, 2015b; Zhang *et al.*, 2017; Bi *et al.*, 2004). The tree-level method involves an independent modelling to estimate total-tree biomass directly, but lacks accurate information of stem, branches, and foliage biomass. The structural component-level, represents also an independent modelling and, total-tree biomass is obtained by summing up the biomass estimation by tree structural components. However, summing up the biomass estimation of structural components can diverge from total-tree biomass. Therefore, the additive method that consists in fitting the biomass data by structural components simultaneously, eliminates the inconsistency of the sum of the biomass by structural tree components on the same sampled trees. Thus, the total-tree biomass is the sum of the biomass of structural tree components.

Many studies mentioned that in tropical natural forests where hundreds of species coexist per hectare it is impractical to represent each specie with its own allometric biomass equation (Pappoe *et al.*, 2010;

Gibbs *et al.*, 2007). While other authors indicate that specific-species can provide more accurate estimates of biomass and that help reflect better the real biomass in species-rich tropical ecosystems (Fehrmann and Kleinn, 2006; Henry *et al.*, 2010; Kebede and Soromessa, 2018; Chaturvedi *et al.*, 2012). Specific-species equations are critical to evaluate the productivity of secondary tropical forests through tracking changes in the biomass stocks (Navar, 2009c; van Breugel *et al.*, 2011; Cai *et al.*, 2013; Cairns *et al.*, 2003). Also, are key tools to understand the role of secondary tropical forests in the global carbon cycle through biomass estimations needed for accurate determination of carbon storage and fluxes (Litton and Boone, 2008; Navar, 2009c). In tropical regions, specific-species equations have been generated mainly for commercial species (Singh *et al.*, 2011; Cai *et al.*, 2013; Zhang *et al.*, 2017). For natural forests they are scarce, but currently there are many works carried out in Costa Rica, Brazil, and India (Segura and Kanninen, 2005; Chaturvedi *et al.*, 2012; Araújo *et al.*, 2018). In Mexico, the species specific equations have been generated in temperate and warm tropical forests stands by Navar (2009c), Douterlungne *et al.* (2013), Cairns *et al.* (2003), and Vargas-Larreta *et al.* (2017). Particularly, Cairns *et al.* (2003) generated 15 equations for species-specific in forests of southern Yucatán peninsula: nine for trees with DBH ≤ 10 cm, six for trees > 10 cm in DBH; as well they generated aa generic equation for tree species with DBH > 10 cm. The range of applicability of the equations developed by Cairns *et al.* (2003) for trees ≤ 10 cm in DBH is limited, due to the high species richness of small-size tree species that characterize the secondary tropical forests in the studied region. Besides, the equations were generated for old-growth stands species. Thus, the generic equation developed by Hughes *et al.* (1999) in the central-east, México, and Chave *et al.* (2003) equation in Panamá are widely used in the tropical forests of México to estimate biomass of trees with DBH ≤ 10 cm. However, the performance Hughes *et al.* (1999) and Chave *et al.* (2003) equations has not yet been evaluated with other equations generated for small-size trees in forests of the Yucatán peninsula. Therefore, the objectives of this study were (1) to develop specific-species equations under an additive system equations approach by tree structural components (stem, branch and foliage) (2) to develop allometric equations for total-tree biomass and (3) to compare the performance of the developed equations on biomass estimation to generalized equations developed for other tropical regions by Hughes *et al.* (1999) and Chave *et al.* (2003). The following hypotheses were tested: a) equations that include the total tree height (TH) and wood density (WD) as independent variables, besides DBH, provide better goodness of fit statistics than simpler equations (*i.e.* based on one or two predictors), since they include in their structure the effect of the allometric characteristics and wood properties that determine the species growth form; and b) specific equations developed in this study are more accurate to estimate total tree biomass at specie level, since it includes the effects biometric characteristics of local species (*i.e.* through DBH, TH and WD), than those generalized equations developed in other tropical regions.

MATERIALS AND METHODS

Study area

This study was conducted across of southeast region of the Yucatán peninsula, Mexico. It is located between the Sian Ka'an Biosphere Reserve in Quintana Roo (19° 05' y 20° 06' north, 87° 30' y 87° 58' west) and Calakmul Reserve in Campeche (19° 15' y 17° 45' north, 90° 10' y 89° 15' west) (Figure 1). The Calakmul Biosphere Reserve is the largest conservation area of rainforest in the Mexican tropics (~ 7, 231.85 km2) (González-Jaramillo *et al.*, 2016). We located secondary tropical forests stands that ranging from nine to 35 years-old and an old-growth stand (more 80-year-old) for tree-biomass harvesting. The stands were used previously for “slash and burn agriculture (maize, beans and squash) system”.

The dominant ecosystem type is mid-stature and semi-evergreen tropical forest (Pennington and Sarukhán, 2005; Miranda and Hernández-Xolocotzi, 1963). The climate is tropical subhumid with mean annual rainfall between 948 and 1500 mm, most of which falls in the summer, while the dry months (april to march) typically have less than 60 mm of rainfall. The mean annual temperature is about 26° C with extremes of 36 °C to 38 °C in the driest months (García, 2003; Lawrence, 2005). There is a hurricane season from June to November, and the highest incidence occurs between August and October (Islebe *et al.*, 2009; McGroddy *et al.*, 2013). The topography is mostly flat with some places with slight inclination. Dominant soils are classified as gleysoles, vertic cambisols and vertic luvisols; they are thin and shallow, resulting in a slow water drainage and surface flooding’s in the rainy season during storms or hurricanes (Ellis and Porter-Bolland, 2008).

Measurements of aboveground biomass

Biomass data was collected from harvesting 311 trees of 22 tree species of 1 cm ≤ DBH ≤ 10 cm (Table 1). The 22 species were selected based on the importance value index-IVI (Curtis and McIntosh, 1951) in a pre-assessment in the same study region. The index-IVI was determined for each species by summing the species relative frequency, relative density, and relative dominance

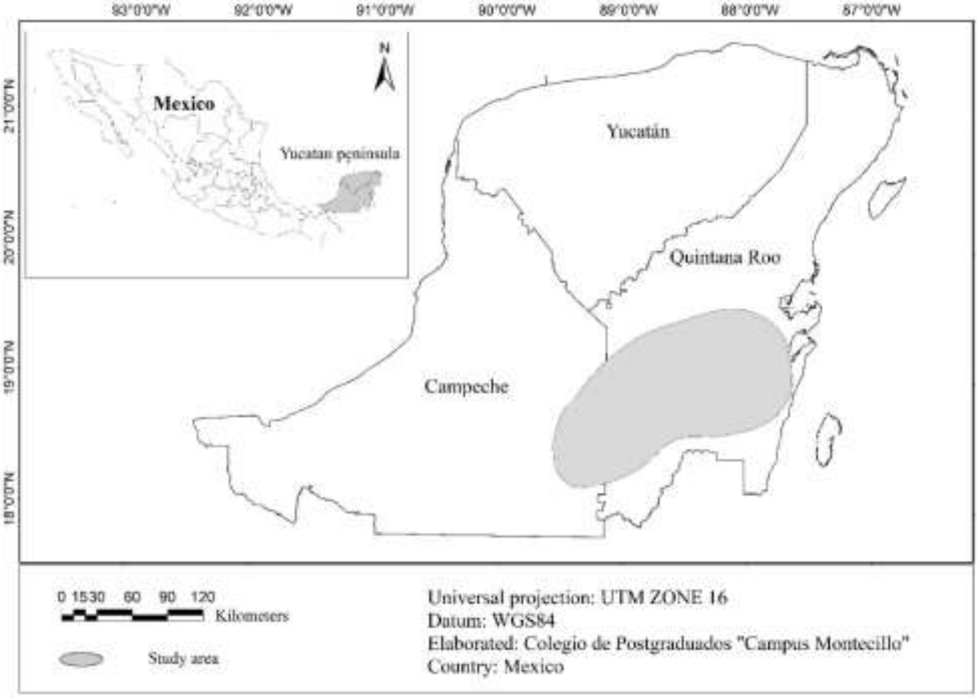

Figure 1. Location of the study site in the southeast Yucatán peninsula.

Table 1. Tree species sampled to fit allometric biomass equations in secondary tropical forests of the southeast Yucatán peninsula.

Species name	N	DBH range (cm)	TH range (m)	Wood density (g cm^{-3})	Class
Lonchocarpus rugosus	13	1.4 - 10	3.1 - 11	0.80 (± 0.03)	H
Pouteria campechiana	14	1.6 – 9.9	2.5 – 11	0.79 (± 0.02)	H
Malmea depressa	13	1.5 – 10	3.1 – 10	0.78 (± 0.01)	H
Pouteria unilocularis	17	1.2 – 10	2.9 – 11.3	0.78 (± 0.01)	H
Chrysophyllum mexicanum	15	1.2 - 9.9	2.7 - 12	0.77 (± 0.01)	H
Lonchocarpus xuul	12	1.4 – 9.9	2.15 – 10.6	0.76 (± 0.02)	H
Psidium sartorianum	13	1.3 – 9.5	2.8 – 13.4	0.75 (± 0.02)	H
Coccoloba diversifolia	13	1.3 – 9.9	1.5 – 11.8	0.74 (± 0.03)	H
Croton reflexifolius	15	1.3 – 9.8	2.8 – 11.2	0.72 (± 0.002)	H
Brosimum alicastrum	14	1.2 – 10	2.8 – 11.2	0.71 (± 0.02)	H
Dipholis salicifolia	18	1.1 – 9.9	2.5 – 10.7	0.69 (± 0.01)	H
Luehea speciosa	12	1.4 – 10	2.8 – 10.4	0.67 (± 0.02)	H
Guettarda combsii	17	1.2 – 10	2.2 – 10.4	0.64 (± 0.01)	H
Swartzia cubensis	14	1.1 – 8.9	2.45 – 11	0.63 (± 0.03)	H
Piscidia piscipula	15	1.2 – 10	2.2 – 10.8	0.62 (± 0.02)	H
Zuelania guidonia	14	1.1 - 10	2.2 – 12.2	0.62 (± 0.01)	H
Lysiloma latisiliquum	15	1.3 – 10	2.6 – 11.2	0.61 (± 0.02)	H
Licaria campechiana	16	1.4 – 9.9	3.2 – 9.6	0.61 (± 0.01)	I
Vitex gaumeri	12	1.2 – 10	2.75 – 10.6	0.52 (± 0.04)	I
Simarouba glauca	14	1.4 – 9.8	2.8 – 9.9	0.42 (± 0.01)	L
Bursera simaruba	12	1.5 – 10	3.1 – 10	0.29 (± 0.02)	L
Cecropia peltata	12	1.1 – 9.9	2.2 – 9	0.25 (± 0.02)	L

N = number of trees; DBH = range in diameter at breast height (cm); TH = range in total tree height (m); wood density in g cm^{-3} = Class= Wood density class (H is hight, I = is intermediate, and L is low).

Based on the index-IVI values, between 12 to 18 trees for each specie were selected and harvested. Before felling the trees, DBH was measured with a diametric tape. After felling, TH (equal to the length of the stem) was measured with a long fiberglass tape. For biomass calculations; fresh weight for each component by tree (*i.e.* stem, branches, and foliage) were obtained with an electronic scale TORREY CRS-HD of 500 kg capacity (± 100 g). Three random samples ~ 100 g of stem, branches, and foliage were obtained with an electronic scale OHAUS Pionner^{tm} 5 kg capacity (accuracy ± 0.1 g), respectively (Wang, 2006; Basuki *et al.*, 2009; Gómez-García *et al.*, 2013). The fresh samples of stem (disks of about 5 cm thick) were cut from the base, middle and upper part of the stem (Bastien-Henri *et al.*, 2010; Picard *et al.*, 2012). To determine WD (g.cm^{-3}), samples were taken from each tree at 1.30 m from the base of the stem (Henry *et al.*, 2010; Nam *et al.*, 2016). The WD was calculated as green volume/dry mass for each sample. The green volume was measured by the water displacement method (Chave *et al.*, 2006). The stem, branches and foliage of trees ≤ 2.5 cm DBH were sent entirely at laboratory. All samples were oven-dried at 70° C until they reached constant dry mass. Dry mass of stem, branches and foliage were calculated on the basis of the fresh mass with the average fresh to dry mass ratio of each component. The total tree aboveground biomass (kg) was calculated by adding up the total dry weight of three structural components of each tree.

The harvested tree species were classified in three WD classes (Table 1) according Sotomayor et al. (Sotomayor *et al.*, 2010): low (≤ 0.40 g. cm^{-3}), intermediate (0.41-0.60 g.cm^{-3}) and high (≥ 0.61 g.cm^{-3}). These classes were used because the density values are associated with the wood quality. Likewise, WD is considered as an economic indicator -for the industry- and a good wood descriptor to study the species ecological behavior (Chave *et al.*, 2006; Sotomayor *et al.*, 2010).

Fitting and evaluation of allometric equations

Total-tree biomass was modeled with independent variables of DBH, TH and WD from eight regression models (Table 2) previously tested in other studies for estimating tree-total biomass (Hughes *et al.*, 1999; Ketterings *et al.*, 2001; Cairns *et al.*, 2003; Bi *et al.*, 2004; Chave *et al.*, 2005; Urquiza-Haas *et al.*, 2007; Chave *et al.*, 2014; Soriano-Luna *et al.*, 2015):

We used an independent fitting to estimates coefficient parameters of models applying the Newton's iterative method with *nls* function and fit technique Ordinary Least Squares (OLS) in R software (R Development Core Team). Weighting regressions were applied to the models to improve the homogeneity of variance and the goodness-fit-statistics (Parresol, 2001; Álvarez-González *et al.*, 2007).

Table 2. Regression models tested to fit allometric biomass equations in secondary tropical forests of the southeast Yucatán peninsula.

No.	Allometric model
1	$\mathrm{AGB} = \exp(-\beta_0)(\mathrm{DBH}^2\mathrm{TH})^{\beta_1} + \varepsilon_i$
2	$\mathrm{AGB} = \beta_0(\mathrm{WDDBH}^2\mathrm{TH})^{\beta_1} + \varepsilon_i$
3	$\mathrm{AGB} = [\beta_0 + \beta_1 \ln(\mathrm{DBH}^2\mathrm{TH})]\left(\frac{\mathrm{WD}}{0.72}\right) + \varepsilon_i$
4	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{WDDBH}^2\mathrm{TH})] + \varepsilon_i$
5	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{DBH}^2\mathrm{TH})] + \varepsilon_i$
6	$\mathrm{AGB} = \exp\left[-\beta_0 + \beta_1 \ln(\mathrm{DBH}^2\mathrm{H}) + \frac{\beta_2}{2}\right] + \varepsilon_i$
7	$\mathrm{AGB} = 0.11\beta_0\mathrm{DBH}^{2+\beta_1} + \varepsilon_i$
8	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{DBH}^2)]\left(\frac{\mathrm{CF}}{10^6}\right) + \varepsilon_i$

AGB = aboveground biomass (kg), β'_S = parameters to be estimated in the fitting process, WD = wood density $(\mathrm{g.cm}^{-3})$, DBH = diameter at breast height (cm); TH = total height (m), and exp = exponential function, ln = natural logarithmic function, CF = correction factor, $\mathrm{CF} = \exp\left(\frac{\mathrm{MSE}}{2}\right)$, MSE = mean square error. We assumed that the error terms are distributed independent and identically distributed as $\varepsilon \sim \mathrm{N}(0, \sigma_e^2)$.

Equation validation and simultaneous fitting

The goodness of fit-statistics: (i) root mean square error of the estimate (RMSE), (ii) the proportion of variance explained by model corrected by the number of parameters estimated (adjusted R^2) and (iii) were used to select the best regression models (Johnson and Omland, 2004; Ngomanda *et al.*, 2014). We used the Akaike Information Criterion (AIC) only to select the best model from Table 2. Overall, the best model was the one which had low (RMSE) and (AIC), and high R^2 (Mugasha *et al.*, 2016).

The best selected model was fitted simultaneously to generate equations by tree structural components. Then, equation for total-tree biomass is a function of the independent variables in the equations for structural component, including constraints on the parameters of the model, and can be expressed as:

$$\mathrm{AGB_{stem}} = \mathrm{f(WD, DBH, TH, \beta)} + \varepsilon_{\mathrm{AGBstem}} \quad (1)$$
$$\mathrm{AGB_{branch}} = \mathrm{f(WD, DBH, TH, \beta)} + \varepsilon_{\mathrm{AGBbranches}}$$
$$\mathrm{AGB_{foliage}} = \mathrm{f(WD, DBH, TH, \beta)} + \varepsilon_{\mathrm{AGBfoliage}}$$
$$\mathrm{AGB_{total-tree}} = \mathrm{f(WD, DBH, TH, \beta)} + \varepsilon_{\mathrm{AGBtotal-tree}}$$

Where:

AGB = above-ground biomass (kg); β = vector of regression parameters to be estimated, DBH = diameter at breast height (cm), TH = total tree height (m), WD = wood density ($\mathrm{g.cm^{-3}}$) for each specie. We assumed that the error terms are distributed independent and identically distributed as $\varepsilon \sim \mathrm{N}(0, \sigma_e^2)$. The parameter vector was calculated using an iterative convergence process with Newton´s algorithm (SAS Institute Inc., 2011). The simultaneous fitting, was performed using the generalized least squares method called nonlinear seemingly unrelated regressions (NSUR) iteratively applying the ITSUR option of PROC MODEL in SAS (SAS Institute Inc., 2011; Sanquetta *et al.*, 2015b). Once the models were fitted and the residuals were obtained, it is very common to detect heteroscedasticity in the residuals (Álvarez-González *et al.*, 2007). In order, to correct this problem, we fitted models using weighted regression to improve homogeneity of variances and guarantee models additivity (Clutter *et al.*, 1983; Parresol, 1999; Magalhães and Seifert, 2015).

Independent modelling

From the selected models, developed also specific-species equations to estimate total-tree biomass. Likewise, we compared total-tree biomass observed against the total-tree biomass estimated with specific-species equations and, generic equations generated by Hughes *et al.* (1999) (2) and Chave *et al.* (2003) (3). Besides, the performance of each equations this study versus the generalized equations of Hughes *et al.* (1999) and Chave *et al.* (2003) was evaluated:

$$\mathrm{AGB} = \exp[4.9375 + 1.0583\ \ln(\mathrm{DBH}^2)]\left(\frac{1.14}{10^6}\right)$$
$$\mathrm{AGB} = \mathrm{WD/WD_{av}}\exp[-1.839 + 2.116\ln(\mathrm{DBH})]$$

Where:

AGB = aboveground biomass (kg), DBH = diameter at breast height (cm), TH = total tree height (m); exp = exponential function, ln = natural logarithmic function, WD = wood density ($\mathrm{g.cm^{-3}}$) and $\mathrm{WD_{av}}$ = wood density mean of the evaluated plot ($0.54\ \mathrm{g.cm^{-3}}$).

We selected the Hughes *et al.* (1999) and Chave *et al.* (2003) generalized equations to evaluate their performance in comparison with equations developed in this study. Hughes *et al.* (1999) and Chave *et al.* (2003) equations were generated for a mixture tree species with DBH ≤ 10 cm, which is the same size range trees used in this study. Hughes *et al.* (1999) equation was developed for a tropical forest in central-east, México, and its application is based only in DBH as biomass predictor variable. Chave *et al.* (2003) equation, also was developed to estimate biomass of small trees in tropical forests of Panamá, it is a re-parametrization of Hughes *et al.* (1999) model, and it includes the WD as a second independent variable, in addition to DBH. We anticipated the addition of WD as biomass predictor to be beneficial for models performance and accuracy. However, let us believe that Hughes *et al.* (1999) and Chave *et al.* (2003) equations has a disadvantage, that its application is limited outside the forests of central-east, México and Panamá owing variables used in both equations are linked or express the biometric characteristics of forest species where the two equations were developed.

Specific-species equations developed in this study, Hughes *et al.* (1999), and Chave *et al.* (2003) equations relative mean error (RME %) was calculated as validation criteria of performance of the allometric models (Djomo *et al.*, 2010; Chave *et al.*, 2014; Goodman *et al.*, 2014) (4):

$$\mathrm{RME}\ (\%) = \left(\sum_{i=1}^{n}\left(\widehat{\mathrm{ABG}}_{\mathrm{Pred}} - \mathrm{ABG_{obs}}\right)/\mathrm{ABG_{obs}}\right) \times 100\Bigg)$$

Where:

$\widehat{\mathrm{AGB}}_{\mathrm{pred}}$ and $\mathrm{AGB_{obs}}$ are the sum of the predicted and observed biomass for each tree species.

The RME (%) were computed using *leave-one-out* cross-validation for specific-species equations developed in this study, and Hughes *et al.* (1999) and Chave *et al.* (2003)) equations (Efron and Tibshirani, 1993). The principle of the *leave-one-out* method was to fit the model from $n-1$ observations and calculate the RME (%) to the observation leave out (data not included in the training) or data validation (Efron and Tibshirani, 1993; Sileshi, 2014). The *leave-one-out* cross-validation was carried out for each species (22 total). Negative and positive values of the RME (%), indicate underestimation and overestimation of the biomass for a set of trees (Kuyah *et al.*, 2012; Goodman *et al.*, 2014). We used Kruskal-Wallis test at 95% confidence intervals with *kruskal.test* function of the "*stats*" package in R (R Development Core Team) to analyze differences in total-tree biomass estimate, and RME (%) values between equations. Furthermore, accuracy of the biomass equations of this study and, Hughes *et al.* (1999) and Chave *et al.* (2003) equations was analyzed with a linear regression between the predicted and observed biomass values (without intercept) using the *lm* function in R (R Development Core Team). If the models correctly fit the data then the slope of the estimated coefficient should be around one; values that are not around one indicates lack of fit of the model (Piñeiro *et al.*, 2008; Sileshi, 2014).

RESULTS

Biomass fitted equations

Results of goodness of fit statistics as modeling performance criteria for total-tree biomass of all data sets (22 tree species) are presented in Table 3. All allometric models fit well to total-tree biomass, and most of them explained more than 90% of the observed biomass variance. Considering the smaller values of RMSE, AIC, and higher R^2, the model I and II showed the best fit compared to the other models. The estimated coefficients parameters were significantly different from zero in all species-specific equations, which suggest that among the variable combined of model I ($\mathrm{DBH^2H}$) and II ($\mathrm{WDDBH^2TH}$) exist a strong relationship with total-tree biomass.

Biomass equations by structural components

The weighting regression $\frac{1}{\mathrm{Dn^2H}}$ was adequate to improve the homogeneity of variance and goodness of fit statistics of the two models. Simultaneous fitting by tree structural component biomass was carried out using the model I structure (Table 4), because it showed the best goodness of fit statistics since the parameter estimates into the system of equations for each specie converged iteratively using the option ITSUR. According to the RMSE an R^2 values, the allometric equations were more accurate for stem and total-tree biomass across 22 species than branch and foliage biomass. The observed biomass variance explained by fitting the model I by tree structural components was: stem, between 64% and 99%; branch, 24% to 95%; foliage, 35% up to 94%, respectively. While, total-tree biomass equations explained 60% to 99% of the total observed biomass variance. Specifically, model I explained less than 70% the observed biomass variance for three components: stem biomass of *Bursera simaruba* (64%); branch biomass in *B. simaruba* (24%) and *Piscidia piscipula* (66%); and, foliage biomass in *Lonchocarpus xuul* (35%), *Zuelania guidonia* (57%) and *Psidium sartorianum* (58%).

Table 3. Goodness of fit statistics for the allometric models fit to 22 tree species ≤ 10 cm diameter of secondary tropical forests of southeast Yucatan peninsula.

No.	Allometric model	RMSE	R^2	AIC
1	$\mathrm{AGB} = \exp(-\beta_0)(\mathrm{DBH^2TH})^{\beta_1} + \varepsilon_i$	11.15	0.94	1509.87
2	$\mathrm{AGB} = \beta_0(\mathrm{WDDBH^2TH})^{\beta_1} + \varepsilon_i$	11.35	0.93	1511.81
3	$\mathrm{AGB} = [\beta_0 + \beta_1 \ln(\mathrm{DBH^2TH})]\left(\frac{\mathrm{WD}}{0.72}\right) + \varepsilon_i$	11.76	0.93	1520.21
4	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{WDDBH^2TH})] + \varepsilon_i$	13.98	0.92	1570.87
5	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{DBH^2TH})] + \varepsilon_i$	14.06	0.92	1572.56
6	$\mathrm{AGB} = \exp\left[-\beta_0 + \beta_1 \ln(\mathrm{DBH^2H}) + \frac{\beta_2}{2}\right] + \varepsilon$	16.64	0.91	1620.51
7	$\mathrm{AGB} = 0.11\beta_0 \mathrm{DBH}^{2+\beta_1} + \varepsilon_i$	17.05	0.91	1626.69
8	$\mathrm{AGB} = \exp[\beta_0 + \beta_1 \ln(\mathrm{DBH^2})]\left(\frac{\mathrm{CF}}{10^6}\right) + \varepsilon_i$	11.56	0.82	1516.91

AGB = aboveground biomass (kg), β_S' = parameters to be estimated in the fitting, ρ = wood density ($\mathrm{g.cm^{-3}}$), DBH = diameter at breast height (cm); TH = total height (m), and exp = exponential function, ln = natural logarithmic function, CF = correction factor, $\mathrm{CF} = \exp\left(\frac{\mathrm{MSE}}{2}\right)$, MSE = mean square error. We assume that the error terms are distributed independent and identically distributed as $\varepsilon \sim N(0, \sigma_e^2)$.

Table 4. Biomass equations and goodness of fit statistics by tree structural components for mall-size trees (≤ 10 cm DBH) in secondary tropical forests of southeast Yucatán peninsula.

Biomass equation	RMSE	R^2	Biomass equation	RMSE	R^2
Coccoloba diversifolia			*Chrysophyllum mexicanum*		data
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.124681)(\mathrm{DBH}^2\mathrm{TH})^{0.899196}$	1.66	0.97	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.685836)(\mathrm{DBH}^2\mathrm{TH})^{0.983545}$	1.34	0.98
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-5.709513)(\mathrm{DBH}^2\mathrm{TH})^{1.180671}$	1.90	0.85	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.202349)(\mathrm{DBH}^2\mathrm{TH})^{0.933029}$	0.88	0.95
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.430226)(\mathrm{DBH}^2\mathrm{TH})^{0.775745}$	0.40	0.88	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.086912)(\mathrm{DBH}^2\mathrm{TH})^{0.737239}$	0.45	0.87
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.99	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.81	0.98
Malmea depressa			*Psidium sartorianum*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-2.860974)(\mathrm{DBH}^2\mathrm{TH})^{0.883201}$	1.07	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.257887)(\mathrm{DBH}^2\mathrm{TH})^{0.961469}$	2.37	0.93
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.024928)(\mathrm{DBH}^2\mathrm{TH})^{0.931261}$	1.27	0.88	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.778556)(\mathrm{DBH}^2\mathrm{TH})^{0.960902}$	1.68	0.92
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.149323)(\mathrm{DBH}^2\mathrm{H})^{0.59191}$	0.47	0.67	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.490508)(\mathrm{DBH}^2\mathrm{TH})^{1.00122}$	0.70	0.58
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.99	0.97	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.26	0.98
Piscidia piscipula			*Lonchocarpus rugosus*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.215632)(\mathrm{DBH}^2\mathrm{TH})^{0.912652}$	1.00	0.99	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.509758)(\mathrm{DBH}^2\mathrm{TH})^{0.997215}$	1.43	0.98
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.672663)(\mathrm{DBH}^2\mathrm{TH})^{0.99452}$	2.44	0.66	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.530371)(\mathrm{DBH}^2\mathrm{TH})^{1.025384}$	1.41	0.92
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.849742)(\mathrm{DBH}^2\mathrm{TH})^{0.798602}$	0.48	0.70	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.900705)(\mathrm{DBH}^2\mathrm{TH})^{0.818951}$	0.20	0.94
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	3.32	0.95	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.51	0.99
Pouteria campechiana			*Luehea speciosa*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.795674)(\mathrm{DBH}^2\mathrm{TH})^{1.009806}$	1.93	0.96	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.832639)(\mathrm{DBH}^2\mathrm{TH})^{1.002754}$	1.84	0.96
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.151849)(\mathrm{DBH}^2\mathrm{TH})^{0.791289}$	1.53	0.84	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.422181)(\mathrm{DBH}^2\mathrm{TH})^{0.951072}$	1.00	0.92
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.306817)(\mathrm{DBH}^2\mathrm{TH})^{0.760773}$	0.44	0.75	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.434142)(\mathrm{DBH}^2\mathrm{TH})^{0.0732}$	0.23	0.86
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.42	0.97	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	3.05	0.95
Swartzia cubensis			*Licaria campechiana*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.749144)(\mathrm{DBH}^2\mathrm{TH})^{1.020441}$	0.97	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.393522)(\mathrm{DBH}^2\mathrm{TH})^{0.929611}$	0.75	0.98
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.722729)(\mathrm{DBH}^2\mathrm{TH})^{0.847592}$	1.04	0.82	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.731634)(\mathrm{DBH}^2\mathrm{TH})^{1.137827}$	1.49	0.95
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.472306)(\mathrm{DBH}^2\mathrm{TH})^{0.70327}$	0.18	0.86	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.314631)(\mathrm{DBH}^2\mathrm{TH})^{0.928314}$	0.63	0.94
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.45	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.10	0.98
Simarouba glauca			*Croton reflexifolius*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.209234)(\mathrm{DBH}^2\mathrm{TH})^{0.855711}$	1.04	0.95	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.439344)(\mathrm{DBH}^2\mathrm{TH})^{0.959533}$	1.77	0.96
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-5.767766)(\mathrm{DBH}^2\mathrm{TH})^{1.196315}$	1.40	0.83	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.486505)(\mathrm{DBH}^2\mathrm{TH})^{0.88975}$	1.16	0.95
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.876313)(\mathrm{DBH}^2\mathrm{TH})^{0.701125}$	0.37	0.81	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.716394)(\mathrm{DBH}^2\mathrm{H})^{0.690435}$	0.36	0.88
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.83	0.96	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.98	0.98
Brosimum alicastrum			*Zuelania guidonia*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.318339)(\mathrm{DBH}^2\mathrm{TH})^{0.921847}$	0.66	0.99	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.358934)(\mathrm{DBH}^2\mathrm{TH})^{0.948296}$	2.13	0.95
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.113012)(\mathrm{DBH}^2\mathrm{TH})^{0.957334}$	1.54	0.88	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.980664)(\mathrm{DBH}^2\mathrm{TH})^{0.913368}$	1.18	0.91
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.886258)(\mathrm{DBH}^2\mathrm{TH})^{0.754311}$	0.35	0.94	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.3396)(\mathrm{DBH}^2\mathrm{TH})^{0.5804}$	0.53	0.57
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.36	0.97	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.52	0.97
Guettarda combsii			*Lysiloma latisiliquum*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.73279)(DBH^2\mathrm{TH})^{0.996919}$	2.13	0.93	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-4.7631)(DBH^2\mathrm{TH})^{1.104133}$	2.29	0.90
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-5.004871)(DBH^2\mathrm{TH})^{1.103206}$	1.26	0.94	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.072008)(DBH^2\mathrm{TH})^{0.90777}$	1.79	0.76
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.979851)(DBH^2\mathrm{H})^{1.039449}$	0.45	0.85	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.36503)(DBH^2\mathrm{TH})^{0.880951}$	0.58	0.60
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{AGB}_i$	1.46	0.99	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{AGB}_i$	2.11	0.96
Lonchocarpus xuul			*Vitex gaumeri*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.210394)(\mathrm{DBH}^2\mathrm{TH})^{0.948648}$	1.08	0.99	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.828804)(\mathrm{DBH}^2\mathrm{TH})^{0.9662}$	1.83	0.93
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.707644)(\mathrm{DBH}^2\mathrm{TH})^{0.965325}$	3.45	0.75	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-5.986197)(\mathrm{DBH}^2\mathrm{TH})^{1.246886}$	1.20	0.94
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-4.73622)(\mathrm{DBH}^2\mathrm{TH})^{0.873947}$	1.05	0.35	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.023044)(\mathrm{DBH}^2\mathrm{TH})^{0.939103}$	0.86	0.75
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	5.13	0.92	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	0.68	0.99
Dipholis salicifolia			*Pouteria unilocularis*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.309925)(\mathrm{DBH}^2\mathrm{TH})^{0.926269}$	1.12	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-3.27356)(\mathrm{DBH}^2\mathrm{TH})^{0.946922}$	1.35	0.98
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.996604)(\mathrm{DBH}^2\mathrm{TH})^{0.934711}$	2.29	0.77	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-3.986981)(\mathrm{DBH}^2\mathrm{TH})^{1.003814}$	1.85	0.94
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.276665)(\mathrm{DBH}^2\mathrm{TH})^{0.584744}$	0.50	0.69	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-3.887617)(\mathrm{DBH}^2\mathrm{TH})^{0.748158}$	0.65	0.80

$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.66	0.98	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	2.50	0.98
Bursera simaruba			*Cecropia peltata*		
$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-4.409187)(\mathrm{DBH}^2\mathrm{TH})^{1.052114}$	2.59	0.64	$\widehat{\mathrm{AGB}}_{\mathrm{s}} = \exp(-4.191628)(\mathrm{DBH}^2\mathrm{TH})^{0.955756}$	0.43	0.98
$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.045752)(\mathrm{DBH}^2\mathrm{TH})^{0.819727}$	1.04	0.24	$\widehat{\mathrm{AGB}}_{\mathrm{b}} = \exp(-4.762545)(\mathrm{DBH}^2\mathrm{TH})^{0.98704}$	1.05	0.84
$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-5.744795)(\mathrm{DBH}^2\mathrm{TH})^{0.864666}$	0.12	0.88	$\widehat{\mathrm{AGB}}_{\mathrm{f}} = \exp(-6.308533)(\mathrm{DBH}^2\mathrm{TH})^{0.92592}$	0.13	0.83
$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	4.05	0.60	$\widehat{\mathrm{AGB}}_{\mathrm{total}} = \sum \widehat{\mathrm{AGB}}_{\mathrm{i}}$	1.49	0.95

$\mathrm{DBH} =$ diameter at breast height (cm); $\mathrm{TH} =$ total tree height (m), $\widehat{\mathrm{AGB}}_{\mathrm{s}}$ =stem biomass estimate (kg), $\widehat{\mathrm{AGB}}_{\mathrm{b}}$ =branch biomass estimate ($\mathrm{kg\,tree}^{-1}$), $\widehat{\mathrm{AGB}}_{\mathrm{f}}$ =foliage biomass estimate (kg), $\widehat{\mathrm{AGB}}_{\mathrm{total-tree}} = \widehat{\mathrm{AGB}}_{\mathrm{s}} + \widehat{\mathrm{AGB}}_{\mathrm{b}} + \widehat{\mathrm{AGB}}_{\mathrm{f}}$ (kg), RMSE = root mean square error of the estimate, and Adjusted R^2 = proportion of variance explained by model corrected by the number of parameter estimates.

Species-specific biomass equations

The coefficients of the parameter and goodness of fit statistics of the species-specific equations to estimate total-tree biomass are showed in Table 5. We developed the species-specific equations using the structure of model II, because it showed the best goodness of fit statistics to estimate total-tree biomass and the parameter estimates for each specie converged iteratively using the independent fitting approach. Thus, the combined predicting variable $(\mathrm{WDDBH}^2\mathrm{HT})$ captured most part of trees biomass. Additionally, the effect of coefficients $(\hat{\beta}_1)$ that represent the influence of the three variables $(\mathrm{WDDBH}^2\mathrm{HT})$ on the biomass were all significantly different from zero at $\alpha = 0.5$. The R^2 values showed that the explained observed biomass variance by fitted models were between 94% and 99%. Total-tree biomass estimation was less accurate in *B. simaruba*, and *Cecropia peltata*, judged by the RMSE and R^2 values.

Table 5. Biomass equations and goodness of fit statistics for species-specific equations for trees ≤ 10 cm diameter of secondary tropical forests of southeast Yucatan peninsula.

Scientific name	N	Equation	RMSE	R^2
Coccoloba diversifolia	13	$\widehat{\mathrm{AGB}} = 0.05068(\mathrm{WDDBH}^2\mathrm{TH})^{0.99516}$	0.004	0.98
Chrysophyllum mexicanum	15	$\widehat{\mathrm{AGB}} = 0.06227(\mathrm{WDDBH}^2\mathrm{TH})^{0.94917}$	0.004	0.99
Malmea depressa	13	$\widehat{\mathrm{AGB}} = 0.11833(\mathrm{WDDBH}^2\mathrm{TH})^{0.87522}$	0.011	0.97
Psidium sartorianum	13	$\widehat{\mathrm{AGB}} = 0.10630(\mathrm{WDDBH}^2\mathrm{TH})^{0.91959}$	0.006	0.99
Piscidia piscipula	15	$\widehat{\mathrm{AGB}} = 0.07289(\mathrm{WDDBH}^2\mathrm{TH})^{0.94587}$	0.013	0.97
Lonchocarpus rugosus	13	$\widehat{\mathrm{AGB}} = 0.04584(\mathrm{WDDBH}^2\mathrm{TH})^{1.02960}$	0.004	0.99
Pouteria campechiana	14	$\widehat{\mathrm{AGB}} = 0.04838(\mathrm{WDDBH}^2\mathrm{TH})^{1.00241}$	0.007	0.98
Luehea speciosa	12	$\widehat{\mathrm{AGB}} = 0.05259(\mathrm{WDDBH}^2\mathrm{TH})^{0.98285}$	0.009	0.97
Swartzia cubensis	14	$\widehat{\mathrm{AGB}} = 0.07647(\mathrm{WDDBH}^2\mathrm{TH})^{0.95817}$	0.005	0.98
Licaria campechiana	16	$\widehat{\mathrm{AGB}} = 0.07333(\mathrm{WDDBH}^2\mathrm{TH})^{1.02468}$	0.008	0.98
Simarouba glauca	14	$\widehat{\mathrm{AGB}} = 0.08854(\mathrm{WDDBH}^2\mathrm{TH})^{0.95660}$	0.006	0.97
Croton reflexifolius	15	$\widehat{\mathrm{AGB}} = 0.09731(\mathrm{WDDBH}^2\mathrm{TH})^{0.91987}$	0.007	0.98
Brosimum alicastrum	14	$\widehat{\mathrm{AGB}} = 0.08155(\mathrm{WDDBH}^2\mathrm{TH})^{0.92658}$	0.030	0.94
Zuelania guidonia	14	$\widehat{\mathrm{AGB}} = 0.08589(\mathrm{WDDBH}^2\mathrm{TH})^{0.94098}$	0.009	0.98
Guettarda combsii	17	$\widehat{\mathrm{AGB}} = 0.05349(\mathrm{WDDBH}^2\mathrm{TH})^{1.02479}$	0.003	0.99
Lysiloma latisiliquum	14	$\widehat{\mathrm{AGB}} = 0.018884(\mathrm{WDDBH}^2\mathrm{TH})^{1.142107}$	0.005	0.97
Lonchocarpus xuul	12	$\widehat{\mathrm{AGB}} = 0.07166(WD\mathrm{DBH}^2\mathrm{TH})^{0.97387}$	0.029	0.96
Vitex gaumeri	12	$\widehat{\mathrm{AGB}} = 0.05771(\mathrm{WDDBH}^2\mathrm{TH})^{1.00887}$	0.007	0.98
Dipholis salicifolia	18	$\widehat{\mathrm{AGB}} = 0.07512(\mathrm{WDDBH}^2\mathrm{TH})^{0.94434}$	0.005	0.98
Pouteria unilocularis	17	$\widehat{\mathrm{AGB}} = 0.07714(\mathrm{WD\ DBH}^2\mathrm{TH})^{0.96663}$	0.011	0.98
Bursera simaruba	13	$\widehat{\mathrm{AGB}} = 0.1156427(\mathrm{WDDBH}^2\mathrm{TH})^{0.88694}$	0.079	0.95
Cecropia peltata	12	$\widehat{\mathrm{AGB}} = 0.060239(\mathrm{WDDBH}^2\mathrm{TH})^{1.02746}$	0.063	0.96

$\widehat{\mathrm{AGB}}$ = aboveground biomass estimate (kg), WD = wood density $\mathrm{g\,cm}^{-3}$, DBH = diameter at breast height cm, TH = total tree height (m), N = number of sampled trees, RMSE =root mean square error of the estimate, and Adjusted R^2 = proportion of variance explained by model corrected by the number of parameter estimates.

Comparison observed versus estimated total-tree biomass

There was a significant linear relationship between predicted biomass with species-specific equations and observed biomass in most individual species (Figure 2). The correlation values (r) were between 0.96 and 0.99 for all species. Three species showed a slightly underestimated biomass owing to the slope value of linear regression $(\hat{\beta}_1)$ being slightly above to one: *L. xuul* $(y = 1.0119)$, *Simarouba glauca* $(y = 1.01448)$ and *C. peltata* $(y = 1.1577)$ (Figure 2). Across all species, the slope value obtained with Hughes *et al.* (1999) equation was between $y = 1.206581$ and $y = 2.53534$ (Figure 2). With Chave *et al.* (2003) equation the coefficient was between $y = 1.17703$ and $y = 1.99099$ (Figure 2). The results indicate that these two equations underestimated observed biomass observed in the majority of tree species, in particular for species with high and intermediate WD. We obtained statistical differences $(\text{Kruskal}-\text{Wallis test; } \chi^2 = 9.78, \text{d.f} = 2, \text{p} \leq 0.007)$ on the median of estimated biomass among equations of this study and those developed by Hughes *et al.* (1999) and Chave *et al.* (2003) .

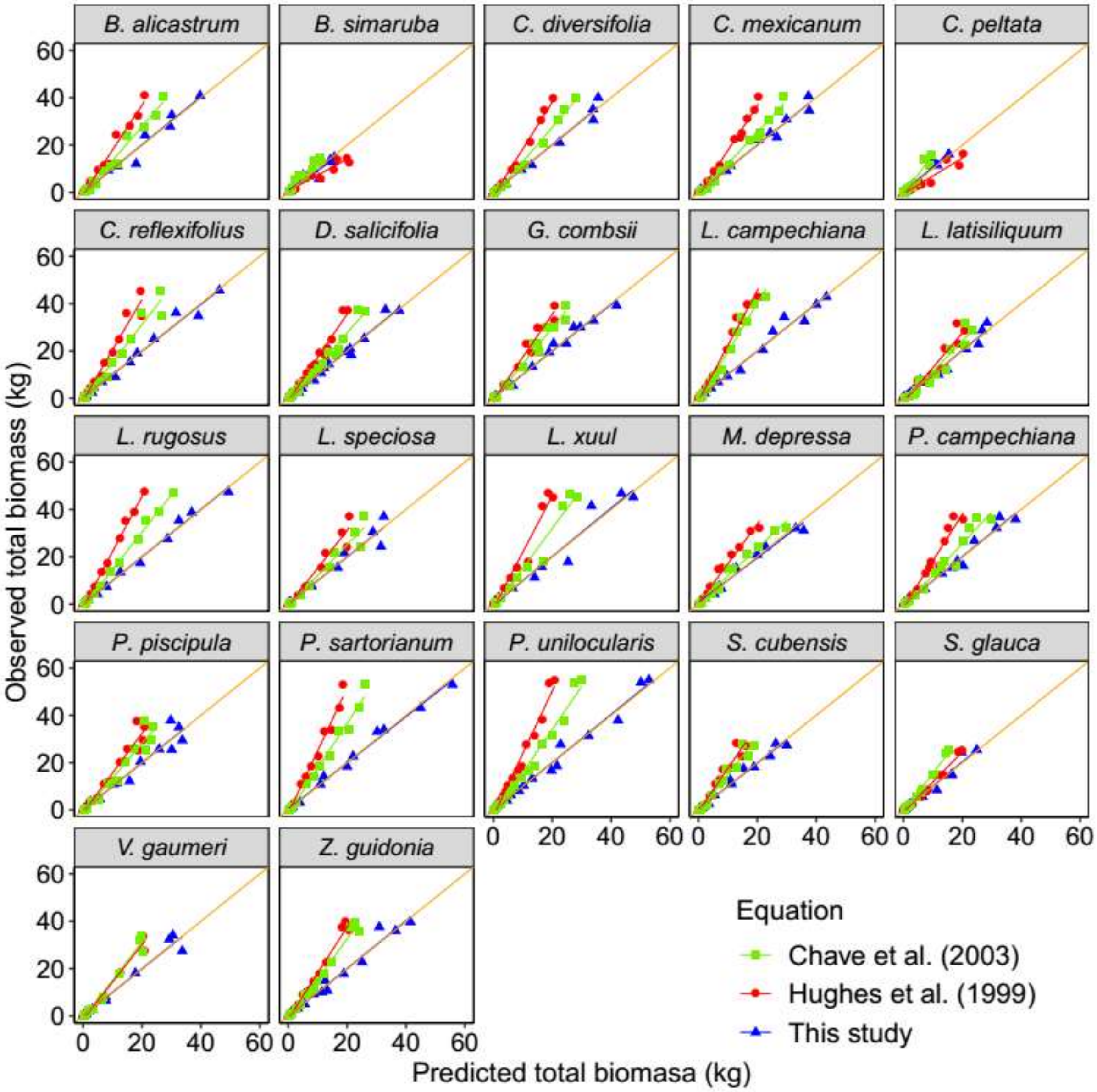

Figure 2. Observed total-tree biomass versus estimated total-tree biomass with species-specific equations fitted in this study, and Hughes *et al.* (1999) and Chave *et al.* (2003) equations. The orange solid line represents the 1:1 ratio between the biomass values. The red, green and blue solid line represents the linear regression between observed and predicted biomass.

Comparison of biomass equations performance

A comparison of the relative mean error (%) of the estimated biomass with the species-specific equations of this study, Hughes *et al.* (1999), and Chave *et al.* (2003) equations is showed in Table 6. Specific-species equations developed in this study overestimated between 0.36% and 2.97% on average the total-tree biomass, which was registered mainly for *Dipholis salicifolia* and *Lysiloma latisiliquum*. While they underestimated total tree-biomass between 0.14% and 9.41% in *Chrysophyllum mexicanum* and *C. peltata*. Chave *et al.* (2003) equation underestimated biomass between 7.38% and 48.46% on average. These values were recorded for *L. latisiliquum* and *Licaria campechiana*, respectively. Besides, Chave *et al.* (2003) equation does not overestimate total tree biomass of any species. When using Hughes *et al.* (1999) equation, an overestimation total tree biomass was observed between 33.04% and 44.22% on average, which corresponded to *B. simaruba* and *C. peltata*. While it underestimated total biomass between 12.10 and 59.82%, and it was observed in *S. glauca*, *Pouteria unilocualris* and *Psidium sartorianum*, respectively. In most of the species, there were significant statistical differences $(\text{Kruskal} - \text{Wallis test};\ \chi^2 = 85.7, \text{d.f} = 2, \text{p} \leq 0.0001)$ in the relative mean error of estimated biomass among equations of this study and, Hughes *et al.* (1999) and Chave *et al.* (2003) equations.

Table 6. Comparison of the relative mean error (%) of the estimated individual total-tree biomass between the species-specific equations developed in this study and those developed by Hughes *et al.* (1999) and Chave *et al.* (2003).

Species name	Hughes *et al.* (1999)	Chave *et al.* (2003)	This study
Brosimun alicastrum	-42.51	-24.49	1.00
Bursera simaruba	33.05	-28.62	1.72
Coccoloba diversifolia	-42.19	-20.86	1.86
Chrysophyllum mexicanum	-42.60	-18.23	-0.15
Croton reflexifolius	-50.77	-34.42	-1.05
Cecropia peltata	44.22	-33.30	-9.42
Dipholis salicifolia	-40.37	-23.87	0.36
Guettarda combsii	-42.56	-32.00	-1.66
Licaria campechiana	-54.33	-48.46	-0.76
Lysiloma latisiliquum	-17.93	-7.38	2.98
Lonchocarpus rugosus	-54.95	-33.33	-2.09
Luehea speciosa	-33.63	-17.73	-0.46
Lonchocarpus xuul	-53.51	-34.64	-1.00
Malmea depressa	-43.32	-18.21	-2.72
Pouteria campechiana	-45.05	-19.70	-0.72
Piscidia piscipula	-35.98	-26.57	-0.19
Psidium sartorianum	-59.82	-44.25	-1.53
Pouteria unilocularis	-55.88	-36.34	1.38
Swartzia cubensis	-42.84	-33.38	-1.66
Simarouba glauca	-12.11	-31.71	0.44
Vitex gaumeri	-30.68	-33.32	-2.72
Zuelania guidonia	-44.43	-36.26	-0.87

DISCUSSION

We developed species-specific equations for estimating biomass by structural components (*i.e.* stem, branch and foliage) and total-tree biomass for small-size trees in secondary tropical forests of the southeast Yucatán peninsula. When we modeled all biomass dataset, the model I and II (Table 2 and 3) presented the best goodness-fit-statistics. The addition of TH and WD in the models as predictors were key variables to improve the models fit. In much of the previous studies, only DBH has been widely used as a predictor variable to fit biomass equations, with which reliable biomass estimates have been obtained in tropical forests (Basuki *et al.*, 2009; Douterlungne *et al.*, 2013; Vargas-Larreta *et al.*, 2017). Other studies use only DBH and WD (Svob *et al.*, 2014; Chaturvedi *et al.*, 2012; Nam *et al.*, 2016), but not TH because of the difficulties that represent to precise measure it in the field (Segura and Kanninen, 2005; Djomo *et al.*, 2010; Hunter *et al.*, 2013). However, our results are consistent con other studies that recognize the need to integrate both TH and WD in models, since they substantially reduce the error in model fitting, and increase the accuracy in biomass estimation (Feldpausch *et al.*, 2012; Chave *et al.*, 2014; Mugasha *et al.*, 2016).

Biomass equations by structural components

Simultaneous fitting of biomass equations by tree structural components were satisfactory with the model I (Table 2), since the total-tree biomass was equal to the sum of the biomass of structural components. Our findings on the additivity of total biomass for individual tree species was consistent with previous studies across the world in temperate forests (Bi *et al.*, 2004; Soriano-Luna *et al.*, 2015; Sanquetta *et al.*, 2015b; Vargas-Larreta *et al.*, 2017; Zhang *et al.*, 2017). In tropical forests, it is not yet frequent studies that fit biomass equations with the simultaneous fitting approach. Besides, other studies have shown that the application of the SUR technique in simultaneous fitting is a successful methodology, because it takes into account the inherent correlations among biomass components to the total-tree biomass (Parresol, 2001; Bi *et al.*, 2010; Dong *et al.*, 2014). While, an independent fitting at component level the sum of components of biomass can generate inconsistent results in total tree biomass, since it does not guarantee the principle of additivity (Sanquetta *et al.*, 2015b; Zhang *et al.*, 2017).

Performance of biomass equations

In tropical forests there are few studies that have compared the equations performance developed for trees ≤ 10 cm DBH. We compare the performance of species-specific equations versus generalized equations by Hughes *et al.* (1999) and Chave *et al.* (2003). Across 22 tree species, species-specific equations developed in this study underestimated ~ 9.5 % on mean total-tree biomass, and overestimated in ~ 3%. Species such as *B. simaruba* showed the higher relative error (Table 6). We observed that the branches of *B. simaruba* were very widespread and of irregular size. Thus, we believe that this pattern of biomass allocation influenced the accuracy of the fit of branch equation of this species (Table 4). It was revealed that branch equations are less accurate since biomass is naturally more variable than the other components (Sanquetta *et al.*, 2015b). For instance, many tropical species and broadleaf species in temperate forests, tend to extend their branches to reach the largest amount of photosynthetic light for tree growth and development (Sanquetta *et al.*, 2015b; Ngomanda *et al.*, 2014; Zhang *et al.*, 2017). This implies that the architectural type of the plant can affect the variability of the branch biomass (Ngomanda *et al.*, 2014).

The performance Hughes *et al.* (1999) equation was inconsistent across the 22 species evaluated in this study. For instance, the error of biomass overestimation for species with low WD (*B. simaruba* and *C. peltata*) was ~ 33% up to 44%. While the error of biomass underestimation in species with high WD (mainly *P. unilocularis* and *P. sartorianum*) was ~ 12% to 60%. Hughes *et al.* (1999) equation did not express with accuracy the biomass of species with wood densities different of the species harvested in stands used in this study. We also observed in our study that *B. simaruba* and *C. peltata* showed higher root mean square error (0.079 and 0.063) than the other species. Our results are consistent with studies reported in dry and wet tropical forests of India and Tanzania (Kebede and Soromessa, 2018; Mugasha *et al.*, 2016), which indicated that WD can affect the models fit since it differs among tree genus and species, such as the species with low and high WD of this study.

When we applied the equation developed by Chave *et al.* (2003) to our data, the biomass estimation at species level improved slightly compared to the Hughes *et al.* (1999) equation, possibly due to inclusion the WD in the equation structure. The performance of Chave *et al.*

(2003) equation was variable in the underestimation biomass of all the species (between 7% and 48.5%), regardless of the number of sampled trees per species. The higher error was recorded in species with high WD (0.61-0.80 g.cm^{-3}). Svob *et al.* (2014) pointed out that when the error of the models differs between tree species, independently of the sample size, the equation should not be applied outside the area where they were generated. The high error levels in biomass estimations registered with Hughes *et al.* (1999) and Chave *et al.* (2003) equations, help us to confirm that the use of equations generated for regions different than the site where they are intended to be applied is a significant source of uncertainty in estimating local biomass-carbon stocks (Sileshi, 2014).

Sources of error in biomass equations

The larger bias in biomass estimates with Hughes *et al.* (1999) equation, might be associated to the use of DBH as the only predictor variable, the sample size that was used (66 trees), and the absence of TH and WD as parameters that are linked to forest structural and growth of the species (Svob *et al.*, 2014).. Particularly, most biomass equations based only on DBH as biomass predictor, could represent a significant bias for total-tree biomass estimates (Chaturvedi *et al.*, 2012), since only DBH is insufficient to explain the whole variation of total-tree biomass (Navar, 2009c; Feldpausch *et al.*, 2012). Therefore, if both TH, WD, and crown diameter are considered in model as predictor variables, there may be a stronger relationships total-tree biomass (Navar, 2009c; Ngomanda *et al.*, 2014; Duncanson *et al.*, 2015). For instance, in Kenia and México in tropical forests the species-specific equations that relate biomass to DBH only may reached biases between 4.6% to 18% (Kuyah *et al.*, 2012; Douterlungne *et al.*, 2013). While generic models, the biomass could be overestimated up to 52% in global scale forests (Djomo *et al.*, 2010; Chaturvedi *et al.*, 2012; Chave *et al.*, 2014). In some tree species of forests of Mexico, India, China, and Thailand, the RMSE of models fit with only DBH vary between 0.55 up to 0.65 (Chaturvedi *et al.*, 2012; Douterlungne *et al.*, 2013; Cai *et al.*, 2013; Ounban *et al.*, 2016). This range values were higher compared with RMSE of 0.004 to 0.111 found in this study. We confirmed that TH and WD in our model I improved the RMSE compared to other models tested. The combined variable (WDDBHTH) in model I, also has been applied in tropical forests of Africa, Asia, Panamá, and Brazil (van Breugel *et al.*, 2011; Goussanou *et al.*, 2016; Nam *et al.*, 2016; Lima *et al.*, 2012). Estimates of total-tree biomass at local scale have been reliable. This type of models more accurately estimates local biomass since they are parameterized with local data of TH and WD, which are strongly correlated with the total-tree biomass. For instance, in African and Asian forests, local equations underestimated 10% and overestimated total biomass up to 23.9%. But, if applied pan-tropical equations that include combined variable for estimating biomass at local scale, the bias in biomass estimation can be up to 62% (van Breugel *et al.*, 2011; Bastin *et al.*, 2015; Goussanou *et al.*, 2016). With our models, we obtained ~ 3% on mean error of the biomass underestimation and ~ 9.5 biomass overestimation.

Regarding the influence of sample size on biomass models, van Breugel *et al.* (2011) compared the performance of models with different sample sizes. The authors fitted two generic local models using 244 trees of 26 species in Panamá secondary forests; using for one model only the DBH as independent variable, and DBH and WD for the second model, respectively. When these authors used 80% (195 trees) and 20% (49 trees) of the total sampled trees, the relative mean error of models increased from 4% to 21%. They concluded that to develop an equation that include only DBH, it is necessary a larger sampling size than a model that includes DBH and WD, since the model parameters are systematically sensitive to small sample size. In that sense, the performance of the generic equation of Hughes *et al.* (1999) might be affected by sample size and the lack of TH and WD as predictor variables , which varies among forests at regional scale (Svob *et al.*, 2014; Ketterings *et al.*, 2001; Chave *et al.*, 2006). Likewise, in dry and wet tropical forest of Costa Rica, Svob *et al.* (2014) observed than the performance of biomass models depends of the sample size, since the uncertainty of the biomass estimation increase when number of sampled trees decreased.

Chave *et al.* (2003) included in their equation a constant value of 0.54 g.cm^{-3}, that corresponds to the mean WD obtained from 123 species in tropical forest of Panamá. However, it appears that the wood densities by species were not obtained entirely in the region where the equation was developed. In contrast, wood densities that we used in our study were based on tree samples that we took in the field. The equations developed in this study showed better performance in biomass estimation that those developed by Hughes *et al.* (1999) and Chave *et al.* (2003).Similar results have been found elsewhere when a generic equation developed from a different region is applied at local level. For instance, Ketterings *et al.* (2001) generated equations for specific sites with trees of 5 to 50 cm in DBH (29 trees total) in secondary forests of Sumatra;

further, they contrasted the performance of their equations with those generated at global scale from data collected in a wide range of tropical climatic conditions and tropical vegetation types by Brown (1997). The Ketterings *et al.* (2001) equations , which included WD in addition to DBH, reduced the estimation error of total biomass by 36-51%, but the estimates were significantly higher than those observed when they applied Brown (1997) equation. In other studies, such as the one carried out in Brazilian forests, 10.6% and 14.8% mean estimation error were observed with the pan-tropical equations of Brown (1997) and Chave *et al.* (2005), whereas the local models showed 5.63% mean estimation error (Lima *et al.*, 2012). In southeast Asian forests, 19.8% on mean error was obtained locally, but when regional and global scale equations were used the mean error was from 31.2% to 38.4% (Nam *et al.*, 2016).

The higher relative estimation error showed by biomass equations may be due to several factors: 1) when the equations are fitted with a relatively small sample size, the coefficients are not adequate for other sites where may be higher tree densities and species richness, which may not be similar to the range of tree-diameters used in the equation fit process (Ketterings *et al.*, 2001; van Breugel *et al.*, 2011; Svob *et al.*, 2014); 2) the use of only DBH as predictor variable may not be sufficient to explain the relationship with total tree biomass, because it does not express all the functional and ecological plant features(Feldpausch *et al.*, 2012; Goussanou *et al.*, 2016); 3) the absence of the effect of TH and WD in the equations, can decrease the prediction capability of the developed equations (Feldpausch *et al.*, 2012; Mugasha *et al.*, 2016; Valbuena *et al.*, 2016). It is widely known, the TH and WD vary among tropical regions due to species composition and site characteristics (*i.e.* soil type, forest age, and precipitation), in which both variables can modify the equations coefficients (Chave *et al.*, 2014; Valbuena *et al.*, 2016) and may not be appropriate for sites outside where the equations were developed (Ketterings *et al.*, 2001; Baker *et al.*, 2004; Cai *et al.*, 2013; Mugasha *et al.*, 2016). Therefore, considering TH and WD as explanatory variables in biomass equations is important to account the biomass variation triggered by environment factors (Feldpausch *et al.*, 2012; Mugasha *et al.*, 2016). In this study we did not use mixed-effects models to analyze the effect of species and sites (covariates). However, we reiterate that the fitted equations implicitly take into account in their structure, through $WDDBH^2HT$, information that accounts the variability effect of local species and site environmental conditions. Consequently, we consider that the equations are efficient and statistically reliable for biomass estimate of small trees in study region. On the other hand, these equations are parsimonious and are applicable for inventory data in other similar forest types owing the inclusion of WD and HT in their structure, and can lead to an improvement in biomass estimation in tropical secondary forests with high species richness.

CONCLUSIONS

We generated species-specific biomass equations for small-size trees of 22 species of secondary tropical forests of the Yucatán peninsula. The biomass equations were fitted by structural components such as stem, branch and foliage, and total-tree biomass. . Our results supported the hypothesis that using TH and WD, besides DBH, as predictor variables in the equations can appreciably reduce the error in the goodness of fit statistics, and better explain total-tree biomass variation. The predicting ability of the species-specific equations here developed was higher in the estimation of total-tree biomass at species level than generic equations developed for other tropical regions. Therefore, we confirmed the hypothesis that local species-specific equations are statistically more precise for biomass estimations at individual-tree level, since they account for the allometry variability of tree species of the site. The individual equations are adequate to improve biomass stocks estimations, while, generic equations may deliver higher uncertainties which needs to be considered when they are applied at local scale. Our equations could be used to reduce the uncertainty on biomass-carbon stocks estimations of tropical secondary forests that contain high densities of small-size tree species, such as those commonly present across the Yucatán peninsula. They may be useful for carbon estimation within climate change contexts to evaluate the role of tropical forests in carbon removals and emissions.

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