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Development of equations for predicting Puerto Rican subtropical dry forest biomass and volume

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Abstract

Carbon accounting, forest health monitoring and sustainable management of the subtropical dry forests of Puerto Rico and other Caribbean Islands require an accurate assessment of forest aboveground biomass (AGB) and stem volume. One means of improving assessment accuracy is the development of predictive equations derived from locally collected data. Forest inventory and analysis (FIA) measured tree diameter and height, and then destructively sampled 30 trees from 6 species at an upland deciduous dry forest site near Ponce, Puerto Rico. This data was used to develop best parsimonious equations fit with ordinary least squares procedures and additive models fit with nonlinear seemingly unrelated regressions that estimate subtropical dry forest leaf, woody, and total AGB for *Bucida buceras* and mixed dry forest species. We also fit equations for estimating inside and outside bark total and merchantable stem volume using both diameter at breast height (d.b.h.) and total height, and diameter at breast height alone for *B. buceras* and *Bursera simaruba*. Model fits for total and woody biomass were generally good, while leaf biomass showed more variation, possibly due to seasonal leaf loss at the time of sampling. While the distribution of total AGB into components appeared to remain relatively constant across diameter classes, AGB variability increased and *B. simaruba* and *B. buceras* allocated more carbon into branch biomass than the other species. When comparing our observed and predicted values to other published dry forest AGB equations, the equation developed in Mexico and recommended for areas with rainfall >900 mm/year gave estimates substantially lower than our observed values, while equations developed using dry forest data from forest in Australia, India and Mexico were lower than our observed values for trees with d.b.h. <25 cm and slightly higher for trees with d.b.h. >30 cm. Although our ability to accurately estimate merchantable stem volume and live tree AGB for subtropical dry forests in Puerto Rico and other Caribbean islands has been improved, much work remains to be done to sample a wider range of species and tree sizes.
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Keywords: FIA; Subtropical dry forest; Biomass; Stem volume; Puerto Rico; Caribbean; Additive models

1. Introduction

In Puerto Rico, subtropical dry forest life zone (sensu Ewel and Whitmore, 1973) is found in areas with rainfall between 600 and 1100 mm/year at elevations less than 300 m. This forested life zone covers 15% of Puerto Rico, mainly along the south coast and over most of the outlying islands of Vieques, Culebra and Mona (Ewel and Whitmore, 1973). Caribbean island subtropical dry forest covers a broad transitional zone between subtropical moist forest at one rainfall extreme and tropical dry forest at the other (Ewel and Whitmore, 1973). As a result, this life zone encompasses a variety of vegetation and forest types with species of varying degrees of deciduousness and growth form. This study focuses on a forest type within the larger subtropical dry forest life zone that typically has greater biomass accumulation in larger, better developed trees, the upland deciduous forest type (Murphy et al., 1995).

Native tree species typically found in the upland deciduous dry forest in Puerto Rico and much of the Caribbean include *Bursera simaruba* (L.) Sarg.; *Bucida buceras* L., *Gymnanthes lucida* Sw., *Exostema caribaeum* (Jacq.) J.A. Schultes; *Guaiacum officinale* L., *Guaiacum sanctum* L., *Pisonia albida* (Heimerl) Britt. ex Standl.; *Pictetia aculeata* (Vahl) Urban; *Acacia macracantha* Humb. and Bonpl., *Capparis* spp. and

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Coccoloba spp. among many others (Ewel and Whitmore, 1973; Little and Wadsworth, 1989; Murphy et al., 1995).

Besides natural variability, disturbance has dominated subtropical dry forest development since European colonization of the islands, and on mainland Puerto Rico, only 4% of the original dry forest remains (Murphy et al., 1995). Human uses of dry forest areas in Puerto Rico have included sugar cane production, livestock grazing, irrigated agricultural crops and fruit trees, urbanization, industrialization and live fire military exercises in parts of Vieques and Culebra. Naturalized species often dominate highly disturbed Caribbean subtropical dry forests and include *Prosopis juliflora* (Sw.) DC., *Parkinsonia aculeata* L., *Tamarindus indica* L., *Acacia farnesiana* (L.) Willd., *Melicoccus bijugatus* Jacq. and *Leucaena leucocephala* (Lam.) DeWit. (depending on authority, *L. leucocephala* is considered either native or naturalized) (Ewel and Whitmore, 1973; Little and Wadsworth, 1989).

Murphy and Lugo (1986), working in subtropical dry forest of the Guánica Commonwealth Forest, found that the basal area of all trees with d.b.h. (stem diameter at 1.37 m) $\geq$2.5 cm averaged 19.8 m^2/ha on 12,173 stems/ha, and there was 44.75 Mg/ha of AGB in all living vegetation. The largest tree sampled had a d.b.h. <25 cm and 97% of the stems had d.b.h. <10 cm (Murphy and Lugo, 1986). Over 40% of the trees had heights between 3 and 4 m, with the overstory canopy height averaging 9 m (Murphy and Lugo, 1986, 1990).

Carbon accounting, forest health monitoring, and sustainable management of these forests require an accurate assessment of the tree biomass and wood volume. Early inventories of Puerto Rico excluded dry forests even though they comprise a substantial portion of the island's forests because they were not considered to have the productive capacity to support commercial wood production (Birdsey and Weaver, 1982; Franco et al., 1997). Current inventories include all forest types regardless of their productive capacities, so resource reports will include estimates of live tree AGB and wood volume and for forest types where these resources were not previously considered.

However, no locally developed allometric equations for estimating AGB in Puerto Rico's dry forests have been available, so estimates were made using equations developed from international data sets, principally Brown (1997) whose equation uses d.b.h. to estimate AGB, from Martínez-Yrízar et al. (1992) which uses basal area as the explanatory variable. Brown (1997) equations were developed from 2 datasets from India of 29 trees with d.b.h. ranging from 3.7 to 39.2 cm, and the author states that these equations should be used for dry forest in zones with rainfall >900 mm/year. Brown (1997) recommends the use of equations from Martínez-Yrízar et al. (1992) for dry forests in zones with rainfall <900 mm/year. Martínez-Yrízar et al. (1992) harvested 191 trees with d.b.h. ranging from 3.0 to 44.9 cm in a single 1000 m^2 plot in dry tropical deciduous forest in Mexico. However, their equation does not take into account leaf biomass (Martínez-Yrízar et al., 1992). Forests classified as subtropical dry in Puerto Rico occur in areas with rainfall that ranges from 600 to 1400 mm/year (Ewel and Whitmore, 1973), so AGB estimates would have to be made with at least two of the three equations.

Using forest inventory data collected from 2001 to 2003 and the equations of Brown et al. (1989), Brown (1997) and Martínez-Yrízar et al. (1992), Brandeis and Suárez-Rozo (2005) found Puerto Rican dry forest AGB that ranged from 33.9 to 76.5 Mg/ha, an average of 11.6 m^2/ha of basal area on 4174 trees with d.b.h. >2.5 cm. The importance of trees with d.b.h. <10.0 cm in dry forest surveyed in the island-wide FIA inventory should be noted. Saplings (trees with $2.5 \geq$ d.b.h. ≤ 12.4) contributed 50.9% of the AGB, 63.3% of the basal area and 94.5% of the stem density (Brandeis and Suárez-Rozo, 2005). Brandeis and Suárez-Rozo (2005) concluded that for dry forest, equations from Martínez-Yrízar et al. (1992) estimated AGB densities which were similar to those found in the dry Guánica Commonwealth Forest, which has an average annual rainfall of 860 mm (Murphy and Lugo, 1986). They also concluded that the equation in Brown (1997) could be considered for estimating AGB in Caribbean subtropical dry forests with higher annual rainfalls. Brandeis and Suárez-Rozo (2005) concluded that accurate per hectare AGB estimates in Puerto Rico need to include saplings with d.b.h. <10 cm because they make up a significant portion of the total subtropical dry forest AGB, and that estimating AGB in larger trees will be erratic and imprecise until more, larger trees have been sampled and that data included in deriving new allometric equations.

The lack of predictive equations hinders accurately estimating of subtropical dry forest wood volume as well. Total stem volume outside bark is used by the United Nations' Food and Agriculture Organization's Forest Resource Assessment when reporting on forest cover and condition worldwide, while merchantable stem volume inside bark is used by the U.S. Department of Agriculture (USDA) Forest Service's FIA program for their reporting. Volume equations have been developed for Puerto Rican subtropical moist forest, subtropical wet forests and plantation-grown species (Wadsworth, 1949; Francis, 1988, 1989; Bauer and Gillespie, 1990; Brandeis et al., 2005), and volume equations were developed for plantation-grown *B. buceras* L. trees (Francis, 1988). In the Puerto Rican forest inventories conducted in 1980 (Birdsey and Weaver, 1982; Franco et al., 1997) and 1990 (Birdsey and Weaver, 1982; Franco et al., 1997) field crews took multiple diameter and height measurements along the bole of each tree so that merchantable stem volume inside bark could be calculated by applying a geometric formula to different bole sections. Subsequently, volume equations were derived from Puerto Rican forest inventory data by first directly calculating stem volume using a geometric formula, then regressing stem volume on diameter at d.b.h. and total tree height (H_T) (Brandeis et al., 2005). However, as previously mentioned past forest inventories did not include dry forests, so volume equations could not be derived from past inventory data sets for that forest type. Despite having detailed and current forest inventory data we have been unable to accurately estimate live tree AGB and merchantable stem volume for subtropical dry forest life zone of Puerto Rico.

In this study, we outline the procedures taken to develop regression equations that use measurements of d.b.h. and H_{T} in the best parsimonious models using ordinary least squares (OLS) and additive models fit with nonlinear seemingly unrelated regressions (NSUR) to estimate subtropical dry forest leaf, woody and total AGB. Volume equations were developed to estimate merchantable (stem volume to a 10 cm upper stem diameter) and total (stem volume in the entire stem) volume, both inside and outside bark from measurements of d.b.h. and H_{T}. Variations in biomass partitioning between leaf, branch and bole compartments of the tree by species and stem diameter class are explored. We also compare the biomass predictions made with these new equations to estimates made using previously published equations developed from dry forest data from other parts of the world to assess if the equations developed from locally obtained data are significantly different and therefore more accurate.

2. Methods

2.1. Description of study area

We measured and destructively sampled trees 30 trees from 6 species in subtropical dry forest near the city of Ponce, Puerto Rico (latitude 17°58′37.73″ and longitude 66°40′18.23″) at a site about to be cleared for road construction. The site has an average rainfall of about 650 mm/year (source: Southeast Regional Climate Center). The study area was categorized as mature secondary forest, and based on a single inventory plot installed at the site (see Brandeis, 2003 for details on forest inventory sampling), there was 7.1 m^2/ha of basal area on 2749 stems/ha of trees with d.b.h. $\geq$2.5 cm. Tree species found on the inventory plot were *B. simaruba*, *B. buceras*, *G. lucida*, *Bourreria succulenta* Jacq., *Krugiodendron ferreum* (Vahl) Urban, *Thouinia striata* Radlk, *Zanthoxylum caribaeum* Lam., *Reynosia uncinata* Urban, *Coccoloba microstachya* Willd. and *Thrinax morrisii* H. Wendl.

Access issues and our target sampling requirements made it necessary to sample from an area that encompassed two distinct types of topography and substrate. The upslope section of the study area was on the side of a hill with thinner limestone-derived soil where bedrock was more visible and some rocky outcrops were evident. The lower section had deeper, darker soils primarily derived from alluvial deposits. Trees were noticeably taller on the lower section of the study area, and the largest trees harvested during the field work came from this area (trees with d.b.h. >30 cm). Trees of that size were not present on the upslope section. However, sometimes AGB was higher for trees harvested in the upslope section of the study site than for trees of a similar size harvested in the lower section. This indicates that while the lower section might be slightly more productive and capable of supporting trees of greater diameters than the upslope section, in general the two sections of the study site were similar. A simple *t*-test of the data (biomass of 12 trees in the lower section versus the 16 trees in the upslope section) did not show a significant difference between them, so both sections of the study site were treated as one sample in all subsequent models and analyses.

It was necessary to conduct the destructive sampling during the month of March, when canopy leaf area index was lowest following the period of least precipitation (Murphy et al., 1995), and therefore, leaf biomass estimates may be underestimated for deciduous species.

2.2. Sample tree selection, harvesting and measurement

A target sampling diameter distribution was designed to emulate the diameter distribution of subtropical dry forest island-wide as described by the 2001–2003 Puerto Rico forest inventory (data available upon request from the USDA Forest Service, Southern Research Station, FIA program). The forest inventory data showed that 85.5% of the stems found in dry forest have d.b.h. $\leq$10 cm (Fig. 1). There were only 7 trees with d.b.h. $\geq$40 cm (3 trees at 40 cm, 3 trees at 50 cm and 1 tree at 70 cm out of a total of 532 trees measured) (Fig. 1). Preference was given to sampling trees that would be classified as growing stock according to the USDA Forest Service's FIA guidelines, which is defined as living trees of commercial species classified as sawtimber, poletimber, saplings and seedlings with one-third or more of the gross volume in its saw-log section must meet grade, soundness and size requirements for commercial logs or the tree must have the potential to meet these requirements if it is poletimber size with 12.5 cm $\leq$ d.b.h. $\leq$ 27.5 cm. To ensure sampling of healthy trees with more typical growth forms, trees with abnormal form were avoided. (Guidelines and measurement descriptions appear in the FIA Field Data Collection Manual, Version 1.62 Supplement C for Puerto Rico and the Virgin Islands, which can be downloaded at: http://www.srs.fs.usda.gov/fia/manual/2.0_P2Manual.htm.) While there was the possibility of introducing a bias in favor of better-formed trees because of these sampling guidelines, the scarcity of larger diameter individuals and overall consistently poor form of the trees resulted in a sample that was generally representative of dry forest trees across the landscape.

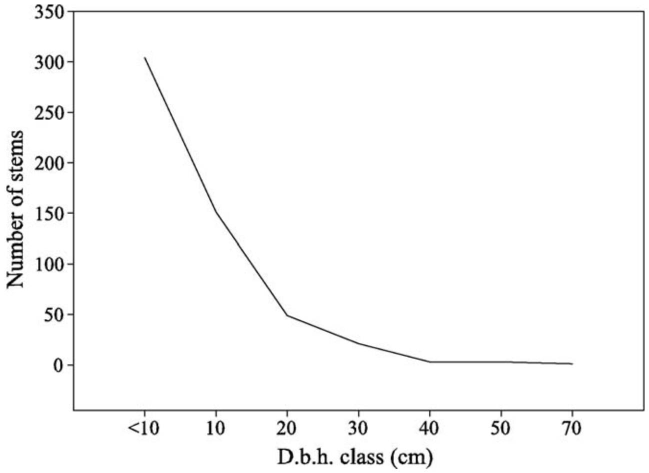

Fig. 1. Stem size distribution in 10 cm diameter classes for subtropical dry forest inventory data on mainland Puerto Rico.

After each tree was felled, the field crew took detailed measurements following the methodology described in Cost (1978) used for developing volume equations in the Southern United States. The measurements included diameter at the base or stump, diameter at d.b.h., diameters every 60–150 cm along the length of the stem depending on bole form, branch diameter and lengths, and total tree height. Bark thickness was sampled each time bole diameter was measured so that inside and outside bark merchantable volume could be estimated. The merchantable bole was defined as the main stem from a 30 cm tall stump to a 10 cm upper stem diameter.

After the felled measurements were taken, the tree was separated into components and each component weighed separately. The first component was the tree's crown, which consisted of leaves, small branches and sometimes seeds and fruits. Time constraints did not allow us to pluck all of the leaves from the crown and weigh them separately. Therefore, we collected all of the small branches (<2.5 cm in diameter) and leaves and weighed them together. In a few cases, no leaves were present on trees that were harvested (5 out of 30 trees, with 3 of those trees not having leaves or twigs; see Table 1). Large branches were defined as any branch with diameter ≥2.5 cm. If a branch was ≥2.5 cm in diameter it was cut and placed in a separate pile for measurement. Sometimes, smaller trees (d.b.h. < 5 cm) did not have any branches that fit that criterion. In these cases, the measured components just consisted of a bole, small branches and leaves. The third component was the main bole. During the field work, there was one case when the main bole was too large to safely handle and place on the scale. In this instance, we measured volume of the pieces and recorded them on the data sheet. The measurements were converted to biomass by applying density (determined by disc samples) to the volume measurements. Usually the chainsaw operator was able to cut the tree down flush with the ground and in these instances no stump was present. However, sometimes a measurable stump was present after a tree was cut down. When this occurred, we measured the stump base, top and height and calculated the stump's volume. We then applied an average density value to calculate stump biomass.

Subsamples were collected to determine the fresh-wet/dry-weight ratio for leaves and branches. The samples were then oven dried and a fresh-weight/dry-weight ratio determined. For the large branches, small branches and leaves, average fresh-weight/dry-weight ratios were applied to the total fresh-weight biomass of each of those components. Sometimes no branch

Table 1
Puerto Rican subtropical dry forest tree diameter at breast height (d.b.h.), total height (m) and aboveground biomass component and total oven-dry weights (kg)

Scientific name	Common name	d.b.h. (cm)	Total height (m)	Leaves and twigs (kg)	Branches (kg)	Bole (kg)	Stump (kg)	Total (kg)
K. ferreum	Bariaco	3.2	3.7	2.0	0.0	2.3	0.0	4.3
K. ferreum	Bariaco	3.7	3.3	1.5	0.0	0.6	0.0	2.1
B. buceras	Úcar	3.8	5.2	5.0	0.0	2.7	0.0	7.7
B. succulenta	Palo de vaca	3.8	6.2	1.9	0.0	2.4	0.0	4.3
K. ferreum	Bariaco	3.9	2.8	3.3	0.0	4.5	0.0	7.9
B. buceras	Úcar	5.4	7.5	2.7	0.0	11.4	0.1	14.3
B. succulenta	Palo de vaca	5.4	6.3	3.2	0.0	7.8	0.0	11.0
G. lucida	Yaití	5.8	6.2	3.1	0.0	10.4	0.0	13.5
K. ferreum	Bariaco	5.8	7.3	4.0	2.4	13.3	0.0	19.7
B. buceras	Úcar	6.4	7.7	6.9	0.0	14.4	1.5	22.7
E. monticola	Birijí	7.7	4.6	2.2	0.0	12.9	0.0	15.1
B. succulenta	Palo de vaca	8.1	8.1	3.6	0.0	15.1	0.0	18.7
B. simaruba	Almácigo	8.5	6.3	0.0	8.8	6.9	0.0	15.7
B. buceras	Úcar	10.3	9.4	9.2	0.0	59.3	0.0	68.5
B. simaruba	Almácigo	10.7	10.6	2.6	0.0	14.4	3.7	20.8
B. simaruba	Almácigo	11.1	5.9	5.3	7.3	7.6	0.0	20.3
B. simaruba	Almácigo	14.2	9.2	8.5	17.2	17.4	0.0	43.1
B. simaruba	Almácigo	17.9	7.8	12.2	24.8	24.4	0.0	61.4
B. buceras	Úcar	18.5	13.7	91.5	39.6	150.4	24.2	305.7
B. buceras	Úcar	19.7	9.4	51.1	74.5	63.9	13.0	202.4
B. simaruba	Almácigo	20.0	11.4	7.7	33.6	32.1	0.0	73.4
B. simaruba	Almácigo	20.3	7.6	0.0	43.4	17.4	4.7	65.5
B. buceras	Úcar	20.7	14.2	48.7	70.6	256.2	0.0	375.4
B. simaruba	Almácigo	20.7	10.1	10.6	65.8	14.2	20.3	110.9
B. buceras	Úcar	22.5	13.4	98.6	37.9	163.3	21.8	321.6
B. simaruba	Almácigo	22.6	7.4	0.0	0.0	64.4	0.0	64.4
B. simaruba	Almácigo	23.2	7.5	0.0	124.7	21.7	0.0	146.4
B. buceras	Úcar	23.2	12.2	63.4	92.7	189.9	98.5	444.5
B. buceras	Úcar	34.5	14.2	129.8	72.1	405.0	11.7	618.6
B. buceras	Úcar	45.0	15.3	244.5	420.2	366.9	72.9	1104.6
Mean values		14.2	8.5	27.4	37.9	65.8	9.1	140.2

Sampled species were *Bourreria succulenta* Jacq., *Bucida buceras* L., *Bursera simaruba* (L.) Sarg., *Eugenia monticola* (Sw.) DC., *Gymnanthes lucida* Sw., and *Krugiodendron ferreum* (Vahl) Urban.

samples were collected for a particular tree because the tree consisted of just a slender bole with just a few small branches and leaves. In these cases, only bole and leaf samples were collected. Wood discs subsamples were cut from the main bole; one disc collected from the top, one disc from the middle and a third collected at the base of the bole. After all three discs were collected, detailed measurements of disc volume were taken, which consisted of two measurements of diameter and two measurements of thickness. After the measurements were taken, each of the discs were placed in cloth bags and labeled. Oven-dry weight was determined by a commercial laboratory. To determine oven-dry weight of the bole, the density results from each of the three discs were applied to the fresh-weight values. After all of the oven-dry weights were determined, the total biomass of the tree was calculated by summing all components.

2.3. Biomass model fitting and estimate comparisons

We used two approaches to modeling biomass data. In the first approach, we sought the best parsimonious model using ordinary least squares procedures models for the leaf, woody and total tree biomass. No consideration is given that the models be additive in nature. That is, the sum of the predicted leaf and the woody biomass do not exactly equal the total predicted biomass for a tree. In the second approach, we sought an additive model where the predicted leaf and predicted woody biomass sum to give exactly the total biomass predicted from the total biomass equation. A desirable feature of tree component regression equations is that the predictions for the components sum to the prediction from the total tree regression. Parresol (1999, 2001) has discussed the problem of forcing additivity on a set of tree biomass functions. The property of additivity assures regression functions that are consistent with each other. That is, if one tree component is part of another component, it is logical to expect the estimate of the part not to exceed the estimate of the whole. Also, if a component is defined as the sum of two subcomponents, its regression estimate should equal the sum of the regression estimates of the two subcomponents. Because of the additivity restriction, the inherent model for $\hat{w}_{\text{total}}$ cannot be linearized. Thus, nonlinear seemingly unrelated regressions must be used as opposed to linear seemingly unrelated regressions by imposing across-equation constraints and fitting the resultant system of equations (Parresol, 2001). This system was fitted with PROC MODEL in SAS software (SAS Institute Inc., 1993).

Observed AGB values, values predicted by our best parsimonious mixed species dry forest model and values predicted by the equations in Brown (1997) and Martínez-Yrízar et al. (1992) were graphed together to facilitate comparison. Since the start of our work, Chave et al. (2005) builds upon and supersedes the work in Brown (1997), so this models estimates were also included for comparison. The dry forest equation in Chave et al. (2005) draws upon data from 404 trees with diameters ranging from 5 to 63.4 cm sampled in Australia, India and Mexico.

These models were:

$$\ln \hat{w}_{\text{total}} = -1.990 + 2.32 \ln (D_{\text{BH}}^2) \quad \text{(Brown, 1997)} \tag{1}$$

$$\hat{w}_{\text{total}} = -0.5352 + \log_{10}(\text{BA}) \quad \text{(Martínez-Yrízar et al., 1992)} \tag{2}$$

$$\hat{w}_{\text{total}} = 0.112 \times (pD_{\text{BH}}^2 H_{\text{T}}) \quad \text{(Chave et al., 2005)} \tag{3}$$

where ln is the natural logarithm, $\hat{w}_{\text{total}}$ the total tree above-ground biomass in oven-dry kg, D_{BH} the diameter at breast height outside bark, H_{T} the total tree height in meters, p the wood specific gravity in g/cm^3, $\log_{10}$ the logarithm and BA is the basal area.

2.4. Volume modeling

Using the detailed measurements taken on each tree, volume estimates (in m^3) were directly calculated by applying the formula for the volume of a conic frustum to bole sections and summing these section volumes for total and merchantable volumes. Total volume is defined here as the inside or outside bark portion of the tree's stem between a 30 cm tall stump and the tip of the tree's stem without a minimum upper diameter merchantability limit. Merchantable volume is defined here as the inside or outside bark portion of the tree's stem between a 30 cm tall stump and a 10 cm upper stem diameter (outside bark). Both total and merchantable volumes exclude wood volume in branches and only refer to main bole volume.

To estimate inside bark merchantable stem volume, the diameters for all sections were converted from outside bark to inside bark. Then, diameters inside bark at stump, breast, saw-log top and pole-top heights were calculated with the following formula for hardwoods:

$$\text{BR} = \frac{D_{\text{BH}} - D_{\text{BT}}}{D_{\text{BH}}} \tag{3}$$

where BR is the bark ratio, D_{BH} the diameter at breast height outside bark and D_{BT} is the double bark thickness.

Section heights and inside and outside bark diameters were used in the formula for a conic frustum to calculate the wood volume of individual sections.

$$V_{\text{SEC}} = \frac{\{H_{\text{SEC}}[D_{\text{IB1}}^2 + (D_{\text{IB1}} D_{\text{IB2}}) + D_{\text{IB2}}^2]0.00007854\}}{3} \tag{4}$$

where V_{SEC} is the section volume in m^3, H_{SEC} the section height in m, D_{IB1} the diameter in cm inside bark at one end of section and D_{IB2} is the diameter in cm inside bark at other end of section.

The constant 0.00007854 is derived from the expression:

$$D_{\text{i}}^2 \left[\frac{\pi}{(4 \times 10,000)} \right] \tag{5}$$

where D_{i} is the section diameter in cm (Husch et al., 1993).

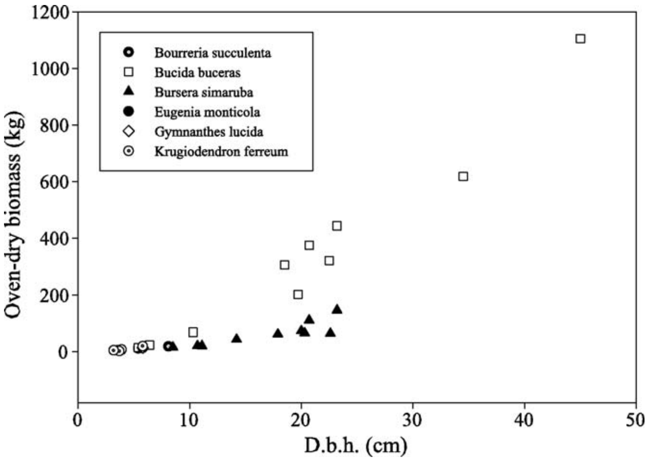

Fig. 2. Total aboveground biomass (oven-dry kg) by stem diameter at breast height (d.b.h.) for each species sampled.

3. Results

Based on the diameter distribution in the forest inventory data, known issues on the degree of variability and influence of larger trees on AGB estimates (Brown et al., 1995; Keller et al., 2001; Chave et al., 2004; Brandeis and Suárez-Rozo, 2005), and the resources available, we set a sampling target of 15 trees in the 10 cm d.b.h. class, 8 trees in the 20 cm d.b.h. class, 5 trees in the 30 cm d.b.h. class and 2 trees in the 40 cm d.b.h. class. These objectives were largely met with the sampling of 18 trees with d.b.h. ranging from 3.2 to 14.2 cm, 11 trees with d.b.h. ranging from 17.9 to 23.2 cm, 1 tree with d.b.h. of 34.5 cm, and 1 tree with d.b.h. of 45.0 cm for a total of 30 trees (Table 1). The lack of larger trees on either section of the site prevented us from sampling more in the 30 and 40 cm d.b.h. classes.

3.1. Biomass models and comparison

The 30 trees we destructively sampled ranged in diameter from 3.2 to 45 cm, and total biomass ranged from 2 to 1100 kg (Table 1 and Fig. 2). Biomass partitioning varied considerably between the species (Fig. 3). Note that the lack of branch biomass for some species is because they were small trees and saplings with few, small (<2.5 cm in diameter) branches. Biomass for these small branches was included in the foliage biomass estimate. The distribution of AGB in the different components remained relatively constant with increasing tree diameter (Fig. 4).

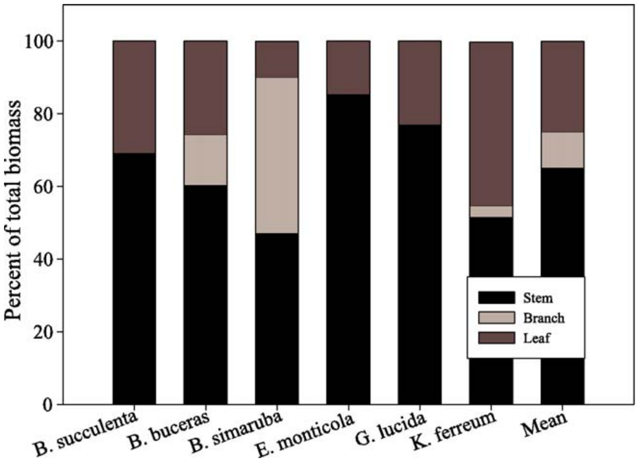

Fig. 3. Percentage of biomass in each tree component (stem, branch and leaf) by species, with mean value.

Fresh-weight/dry-weight ratios varied by tree species and component but overall the averages were similar. The average fresh-weight/dry-weight ratio of all 30 trees was 53% for leaves and small branches, and for medium and large branches the average for all 30 trees was 54%. Wood specific gravity varied by species and ranged from 0.29 to 0.98. The highest average specific gravity was *K. ferreum* at 0.879 g/cm^3 and the lowest was *B. simaruba* 0.31 g/cm^3 (Table 2).

Only two independent variables were available for modeling, diameter (D_{BH}) and total height (H_{T}). This leads to expressions having the functional form $Y = f(D_{\mathrm{BH}}, H_{\mathrm{T}})$. We selected the best biomass component equations based on scatterplots of the data and running all possible regressions on combinations of the variables.

For the dry forest mixed species data ($N = 26$) we settled on the following equations:

$$\hat{w}_{\text{leaf}} = b_1 D_{\mathrm{BH}}^{b_2} \tag{6}$$

$$\hat{w}_{\text{woody}} = b_1 (D_{\mathrm{BH}}^2 H_{\mathrm{T}})^{b_2} \tag{7}$$

$$\hat{w}_{\text{total}} = b_1 (D_{\mathrm{BH}}^2 H_{\mathrm{T}})^{b_2} \tag{8}$$

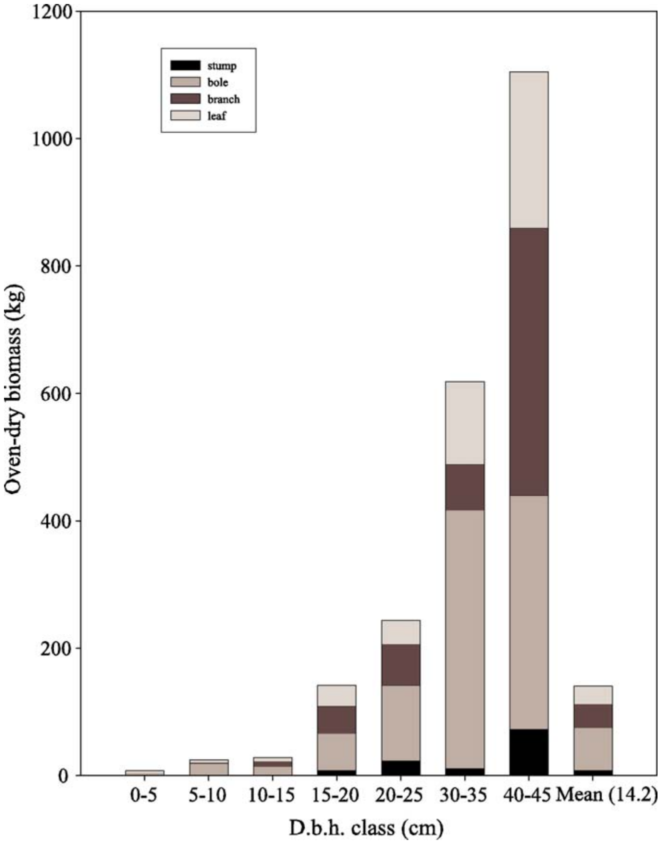

Fig. 4. Component (stem, branch and leaf) biomass by 10 cm diameter classes, with mean value.

Table 2
Wood bole density values averaged by species ($N = 30$) from this study, published in Reyes et al. (1992), and from the World Agroforestry Centre's (WAC) web-accessible database at: http://www.worldagroforestry.org/sea/Products/AFDbases/WD/ (Rahayu, 2005)

Species	Common name	*N*	Study	Reyes et al. (1992)	WAC website
Bucida buceras	Úcar	11	0.79	0.93	0.85
Bursera simaruba	Almácigo	10	0.31	0.29	0.3
Eugenia monticola	Birijí	1	0.71	0.65	–
Krugiodendron ferreum	Bariaco	4	0.87	–	1.2
Bourreria succulenta	Palo de vaca	3	0.54	–	–
Gymnanthes lucida	Yaití	1	0.8	–	–
Average		30	0.67		

where $\hat{w}$ is the biomass in oven-dry kg, D_{BH} the diameter at 1.37 m and H_{T} is the total height.

Scatterplots of the residuals revealed significant heteroscedasticity (as expected). One may want to assume equation errors that are multiplicative to derive log-linear models. The logarithmic transformation tends to stabilize heteroscedastic variance (if σ_ε is proportional to $E[y]$; Neter et al., 1985, pp. 137–138) and is an alternative to deriving weights for each equation. Thus, for the dry forest data we have the following biomass equations:

$$\ln \hat{w}_{\mathrm{leaf}} = b'_1 + b_2 \ln D_{\mathrm{BH}} \tag{9}$$

$$\ln \hat{w}_{\mathrm{woody}} = b'_1 + b_2 \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{10}$$

$$\ln \hat{w}_{\mathrm{total}} = b'_1 + b_2 \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{11}$$

where ln is the natural logarithm, $\hat{w}$ the biomass in oven-dry kg, D_{BH} the diameter at 1.37 m and H_{T} is the total height, $b'_1 = \ln b_1$.

The resulting system of additive equations for the dry forest mixed species data are the following:

$$\ln \hat{w}_{\mathrm{leaf}} = \ln b_{11} + b_{12} \ln D_{\mathrm{BH}} \tag{12}$$

$$\ln \hat{w}_{\mathrm{woody}} = \ln b_{21} + b_{22} \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{13}$$

$$\ln \hat{w}_{\mathrm{total}} = \ln [b_{11} D_{\mathrm{BH}}^{b_{12}} + b_{21} (D_{\mathrm{BH}}^2 H_{\mathrm{T}})^{b_{22}}] \tag{14}$$

where ln is the natural logarithm, $\hat{w}$ the biomass in oven-dry kg, D_{BH} the diameter at 1.37 m and H_{T} is the total height.

For the species *B. buceras* ($N = 11$), the best parsimonious natural logarithm-transformed models are the following:

$$\ln \hat{w}_{\mathrm{leaf}} = b'_1 + b_2 \ln D_{\mathrm{BH}} \tag{15}$$

$$\ln \hat{w}_{\mathrm{woody}} = b'_1 + b_2 \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{16}$$

$$\ln \hat{w}_{\mathrm{total}} = b'_1 + b_2 \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{17}$$

where ln is the natural logarithm, $\hat{w}$ the biomass in oven-dry kg, D_{BH} the diameter at 1.37 m and H_{T} is the total height, $b'_1 = \ln b_1$.

The coefficients and fit statistics for the best parsimonious, natural logarithm-transformed models for dry forest mixed species and *B. buceras* are given in Table 3.

Because of the additivity restriction, the inherent model for $\hat{w}_{\mathrm{total}}$ cannot be linearized. Thus, NSUR must be used as opposed to linear seemingly unrelated regressions. The resulting system of additive equations for the dry forest mixed species data are:

$$\ln \hat{w}_{\mathrm{leaf}} = \ln b_{11} + b_{12} \ln D_{\mathrm{BH}} \tag{18}$$

$$\ln \hat{w}_{\mathrm{woody}} = \ln b_{21} + b_{22} \ln (D_{\mathrm{BH}}^2 H_{\mathrm{T}}) \tag{19}$$

$$\ln \hat{w}_{\mathrm{total}} = \ln [b_{11} D_{\mathrm{BH}}^{b_{12}} + b_{21} (D_{\mathrm{BH}}^2 H_{\mathrm{T}})^{b_{22}}] \tag{20}$$

Table 3
Number of trees sampled (*N*), equations coefficients, mean square error (M.S.E.) and *r*-squared statistic for the ordinary least squares leaf, woody and total aboveground biomass models for mixed, dry forest species and *Bucida buceras*

Component	*N*	b_1	b_2	M.S.E.	r^2
Mixed species					
Leaf	26	−1.75242	1.71833	0.57199	0.75980
Woody	26	−2.87503	0.92900	0.27738	0.92500
Total	26	−1.94371	0.84134	0.25252	0.91750
Bucida buceras					
Leaf	11	−1.47983	1.83142	0.19500	0.92300
Woody	11	−2.68937	0.94081	0.07125	0.98060
Total	11	−1.76887	0.86389	0.03091	0.98990

Table 4
Additive equation for aboveground biomass models for mixed, dry forest species and *Bucida buceras*

	b_{11}	b_{12}	b_{21}	b_{22}
Mixed species	0.307631	1.540044	0.072847	0.899279
Bucida buceras	0.389481	1.665027	0.048955	0.977025

Table 5
Number of trees sampled (*N*), mean square error (M.S.E.) and *r*-squared statistic for additive leaf, woody and total aboveground biomass models for mixed, dry forest species and *Bucida buceras*

Component	*N*	M.S.E.	r^2
Mixed species			
Leaf	26	0.5938	0.7403
Woody	26	0.2729	0.9232
Total	26	0.2488	0.9153
Bucida buceras			
Leaf	11	0.2012	0.9117
Woody	11	0.0713	0.9785
Total	11	0.0395	0.9857

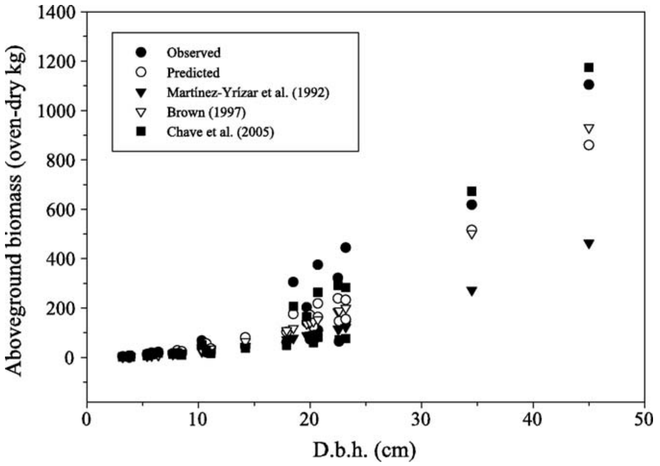

Fig. 5. Observed and estimated values for total aboveground biomass for mixed, subtropical dry species. Predicted values from equations in Chave et al. (2005) and Martínez-Yrízar et al. (1992) and the ordinary least squares equation developed in this study.

where ln is the natural logarithm, $\hat{w}$ the biomass in oven-dry kg, D_{BH} the diameter at 1.37 m and H_{T} is the total height.

The coefficients and fit statistics for additive models fitted to the dry forest mixed species and *B. buceras* are given in Tables 4 and 5. Note the reduction in standard errors on the coefficients from the additive system fit with NSUR when comparing the results in Table 3 against the results in Tables 4 and 5. For example, for dry forest mixed species, the best parsimonious model's coefficient for leaf biomass was $b_2 = 1.718$ (S.E. = 0.197) which corresponds to the NSUR coefficient $b_{12} = 1.540$ (S.E. = 0.163). The reduction in the standard error is (0.197 − 0.163)/0.197 = 0.173 or 17.3%. This results from contemporaneous correlations among the equations and is the reason NSUR is more efficient over using OLS on the individual equations.

Observed AGB values, values predicted by the best parsimonious mixed species dry forest model, and values predicted by the dry forest equations in Brown (1997), Martínez-Yrízar et al. (1992) and Chave et al. (2005) are presented in Fig. 5. The divergence of AGB estimates made with the different equations with increasing d.b.h. is notable.

3.2. Volume models

Volume models were fit to the data using d.b.h. and H_{T} as explanatory variables. Models that use only d.b.h. were also fit to provide a means of estimating volume from data sets that lack height measurements. The following are the final models

Table 6

Number of trees sampled, equation coefficients, mean square error (M.S.E.) and *r*-squared statistic for estimating total and merchantable volume in cubic meters for mixed dry forest species, *Bucida buceras* and *Bursera simaruba* for models using tree d.b.h. (cm) and tree height (m)

Species	*N*	Inside bark				Outside bark			
		b_1	b_2	M.S.E.	r^2	b_1	b_2	M.S.E.	r^2
Total volume[a]									
Mixed	17	−0.0173	0.000047	0.0011	0.9906	−0.0114	0.000046	0.0010	0.9916
Bucida buceras	9	0.0001	0.000047	0.0010	0.9952	0.0002	0.000046	0.0010	0.9950
Bursera simaruba	8	0.0370	0.000028	0.0003	0.8536	0.0354	0.000030	0.0004	0.8312
Merchantable volume[b]									
Mixed	17	−0.0593	0.000046	0.0020	0.9826	−0.0576	0.000045	0.0019	0.9828
Bucida buceras	9	−0.0697	0.000046	0.0024	0.9888	−0.0688	0.000046	0.0023	0.9890
Bursera simaruba	8	0.2890	0.000025	0.0009	0.5553	0.0285	0.000023	0.0009	0.5620

[a] Inside bark portion of the tree's stem between a 30 cm tall stump and the tip of the tree's stem without a minimum upper diameter merchantability limit.

[b] Inside bark portion of the tree's stem between a 30 cm tall stump and a 10 cm upper stem diameter.

Table 7

Number of trees sampled, equation coefficients, mean square error (M.S.E.) and *r*-squared statistic for estimating total and merchantable volume in cubic meters for mixed dry forest species, *Bucida buceras* and *Bursera simaruba* for models using tree d.b.h. (cm)

Species	*N*	Inside bark					Outside bark				
		b_1	b_2	b_3	M.S.E.	r^2	b_1	b_2	b_3	M.S.E.	r^2
Total volume[a]											
Mixed	17	0.1810	0.0234	0.0012	0.0044	0.9662	0.1726	−0.0222	0.0012	0.0036	0.9708
Bucida buceras	9	−0.0182	−0.0018	0.0008	0.0012	0.9951	0.0007	−0.0034	0.0008	0.0012	0.9950
Bursera simaruba	8	−0.2921	0.0340	−0.0006	0.0004	0.8255	−0.2388	0.0273	−0.0004	0.0006	0.8091
Merchantable volume[b]											
Mixed	17	0.0744	0.0182	0.0011	0.0028	0.9771	0.0729	−0.0179	0.0011	0.0027	0.9780
Bucida buceras	9	−0.0991	−0.0009	0.0008	0.0025	0.9897	−0.0949	−0.0011	0.0008	0.0025	0.9899
Bursera simaruba	8	0.0807	−0.0126	0.0007	0.0000672	0.9708	0.0877	−0.0135	0.0007	0.000065	0.9727

[a] Inside bark portion of the tree's stem between a 30 cm tall stump and the tip of the tree's stem without a minimum upper diameter merchantability limit.

[b] Inside bark portion of the tree's stem between a 30 cm tall stump and a 10 cm upper stem diameter.

chosen:

$$\hat{v}_{\text{stem}} = b_1 + b_2(D_{\text{BH}}^2 H_{\text{T}}) \tag{21}$$

$$\hat{v}_{\text{stem}} = b_1 + b_2(D_{\text{BH}}) + b_3(D_{\text{BH}})^2 \tag{22}$$

where $\hat{v}_{\text{stem}}$ is the stem volume in cubic meters, D_{BH} the diameter at 1.37 m and H_{T} is the total height.

The number of trees sampled, equation coefficients, mean square error (M.S.E.) and *r*-squared statistic for estimating inside and outside bark total and merchantable volume in cubic meters for mixed dry forest species, *B. buceras*, and *B. simaruba* for models using d.b.h. and H_{T} are given in Table 6. Statistics and coefficients for inside and outside bark total and merchantable volume estimation models that use only d.b.h. as an explanatory variable are in Table 7.

4. Discussion

Although this study has improved our ability to accurately estimate live tree AGB and stem volume for upland forests in the subtropical dry forest life zone of Puerto Rico and other Caribbean islands that share these species and forest types, work remains to be done. Due to the time-consuming nature of biomass sampling, future sampling that would build on this initial data set should be carefully targeted to provide the largest possible contribution to model improvement.

Our study's sampling emulated the diameter distribution of the forest inventory but probably did not adequately sample larger trees where AGB has been show to become highly variable (Brandeis and Suárez-Rozo, 2005). In the future, we need to lower our threshold for what we would normally consider larger trees down to 25 cm d.b.h., or even 20 cm d.b.h., and sample more of those trees from a wider variety of species to improve the fit of our models and capture variations in growth form and biomass allocation that appear to become more marked as trees increase in size.

The study site had 650 mm of precipitation annually, so the recommended equation for AGB estimation would be that of Martínez-Yrízar et al. (1992) developed in Mexico at a site that has an average rainfall of 707 mm/year. However, even after adding 25% (the average percentage of total AGB that was in leaves and small branches with diameter <2.5 cm in this study), to account for the leaf biomass not sampled by Martínez-Yrízar et al. (1992), this equation estimates AGB to be substantially lower than the observed values, estimates from using the Brown (1997) equation and Chave et al. (2005) equations or estimates from the equations developed in this study. Our additive equations, those of Brown (1997) and those of Chave et al. (2005) underestimated AGB for trees in the 20 cm d.b.h. class (Fig. 5). Our additive equations and those of Brown (1997) still underestimated the biomass in the larger diameter (d.b.h. > 30 cm) trees, while the estimates made using the equations from Chave et al. (2005) were only slightly greater than the observed values for larger trees.

Our models' AGB predictions for larger trees are heavily influenced by *B. buceras*, the only species found in the study area with a d.b.h. ≥30 cm (Fig. 2). This may result in our mixed species models over-estimating AGB at larger diameters for species other than *B. buceras*. For example, there is indication that *B. simaruba*, a tree commonly found throughout Caribbean subtropical dry forest, does not accumulate AGB with increasing d.b.h. as quickly as *B. buceras* (Fig. 2). Additionally, biomass partitioning into leaf, branch and stem components varies considerably among the species sampled, with *B. simaruba* and *B. buceras* investing more into branch biomass than the other species (Fig. 3). Although most of the larger trees sampled were either *B. buceras* or *B. simaruba*, this trend in AGB distribution does not appear to be an artifact of sampling because the distribution of total AGB into components appeared to remain relatively constant across diameter classes.

Although the lack of data for large trees is a common difficulty in biomass modeling, and large trees have been shown to strongly influence stand-level AGB estimates in humid tropical forests (Brown et al., 1995; Keller et al., 2001; Chave et al., 2004), there are also good reasons for not concentrating all our future efforts on sampling large trees alone. Keller et al. (2001) posited that, while the AGB of large trees made up a substantial portion of an area's AGB at the plot and stand level, it was less influential on AGB estimates made across a landscape because large trees are relatively rare at that level. We can expand on the argument made by adding that overall tree size and the frequency of relatively large trees is even less in subtropical dry forest, and therefore large trees may be less influential on stand-level subtropical dry forest AGB estimates than we originally anticipated. Also, we must not focus entirely on less-disturbed upland dry forests where larger trees are more frequently found and neglect to sample the species more typical of heavily disturbed areas that are currently prevalent in the Caribbean subtropical dry forest life zone.

Further sampling is needed to provide data for a wider range of species with potentially differing growth forms and patterns of biomass allocation. Biomass equations for more of the common subtropical dry forest species need to be developed if we are to further improve our ability to estimate AGB and carbon for these forests. This work should be seen as part of an ongoing process, and the equations presented here will be refined as additional sampling adds to the data available.

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