



Composition and aboveground tree biomass of a dry semi-evergreen forest on Mexico's Yucatan Peninsula

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Abstract

Forest biomass estimates are used to help quantify pools and flux of greenhouse gases (e.g., CO₂-C) from the terrestrial biosphere to the atmosphere associated with land-use and land cover changes. Such estimates based on direct measurements are quite limited for tropical dry forests. The goal of this study was to assess the species composition and biomass density in an intact Mexican forest representative of the tropical dry forest biome. We then compared our measured biomass with biomass estimates computed with a published model in current use. A total of 72 species were found in a 0.5 ha stand with a basal area of 31.3 m² ha⁻¹. The dominant species, in terms of biomass, were *Brosimum alicastrum* Sw., *Manilkara zapota* (L.) Royen, *Luehea speciosa* Wildl., *Pouteria unilocularis* (Donn. Sm.) Baehni, *Trichilia minutiflora* Standl., and *Spondias mombin* Linn. Tree heights ranged up to 30 m and dbh to 82.1 cm. Species-specific biomass regression models were developed for the six most common species of large (>10 cm dbh) trees and for the nine most common species of small (<10 cm dbh) trees from the destructive harvest of 698 trees. Mass of large trees ($n = 195$) were used to derive the regression model $Y = \exp\{-2.173 + 0.868 \ln(D^2 TH) + 0.0939/2\}$, where Y is the total dry weight (kg), D the dbh (cm), and TH the total height (m). Total aboveground tree biomass was estimated to be 225 Mg ha⁻¹, and was dominated (85%) by the biomass of the large trees. The actual biomass of each of the 195 large trees was compared to individual tree biomass calculated with a published regression model [Estimating biomass and biomass change of tropical forests. A primer. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome, Italy, 1997] that is based on measurements of 29 trees. We found that the published model underestimated biomass of these trees by 31% (37.6 versus 54.4 Mg). Calculated biomass was less than measured biomass for 29 of 33 species. The current study points to the value of site-specific assessment of aboveground biomass and may contribute to more accurate estimates of dry tropical forest biomass densities currently used to estimate greenhouse gas flux from land management activity.

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1. Introduction

Quantification of biomass is useful for estimating amounts of available forest resources, such as food, fuel, fodder, and fiber (Brown, 1997). Forest biomass data can also be used to understand changes in forest structure resulting from succession or in differentiating between forest types. An important use of biomass density (dry mass/unit area) in recent years has been to track carbon cycling between the atmosphere and the terrestrial biosphere, related to global climate change (Cairns et al., 2000). Biomass change represents the potential for carbon (~50% of dry weight biomass) emissions to the atmosphere when forests are degraded or replaced through processes of deforestation and biomass burning. Conversely, growth results in accumulation of biomass and represents atmospheric CO₂-C sequestration in the terrestrial biosphere. Thus forest biomass can act as either a source or sink for greenhouse gases. Developing global carbon markets, specified in the Kyoto protocol for climate change, require accurate and reliable methods to quantify these sources and sinks.

Tropical forest biomass has been estimated with several methods (Brown and Lugo, 1982, 1984; Olson et al., 1983; Brown et al., 1989; Brown and Iverson, 1992; Gillespie et al., 1992; FAO, 1993). Because of the urgent need for regional and national scale biomass and carbon density data, Brown (1997) reported methods for using existing forest inventory data to estimate biomass densities of tropical forest trees. That report presented biomass regression equations derived from data for harvested trees of many species in tropical forests of four climatic zones (very dry, dry, moist and wet) (Brown, 1997).

Sequestration of C in forest biomass may result from net annual growth increment, and may be significant in young, growing forests. Models are used to quantify C accumulation in such forests (Turner et al., 1995), although these methods are beyond the scope of this paper. Alternatively, changes in spatial extent of forests compared to that of other land cover types, when viewed at different points in time, and coupled with accurate estimates of biomass for each land cover class are used to estimate C pools and flux (Cairns et al., 2000). The dynamics of land-use in the Yucatan has been dominated during the past several decades by net loss of forest cover in favor of agricultural land

uses. In either case, accurate knowledge of the biomass and C content of the forest and other land cover types is essential for understanding the direction and magnitude of C fluxes in terrestrial systems.

Deforestation on the Yucatan Peninsula has increased during the last 15 years because of the pressures of agriculture, cattle ranching, tourism development, and urbanization (Olmsted et al., 1999). Cairns et al. (2000) reported an annual average deforestation rate of 1.9% in an eight-state tropical region of Mexico between 1977 and 1992. There has been a decrease in mature forest and simultaneous increases of non-vegetated areas and secondary vegetation in the Yucatan. To understand carbon sources and sinks, we need biomass estimates for these forests. In the Yucatan Peninsula, biomass data derived from harvested trees are available only for the driest portion, in the state of Yucatan (Mizrahi et al., 1997). Because biomass data based on harvested trees are very scarce, but needed badly, we sought to measure aboveground tree biomass in a medium stature semi-evergreen forest (Miranda, 1964) in the state of Quintana Roo on the Yucatan Peninsula.

The objectives of this paper are: (1) to develop a series of aboveground biomass allometric regression equations for common species occurring in a semi-evergreen forest in Quintana Roo, Mexico; (2) to report a 'global' biomass regression equation to represent all species in this forest type; (3) to compare our measured biomass values with biomass estimates based on a dry tropical forest allometric equation reported in the literature.

2. Methods

2.1. Study site

The study site is located in La Pantera, Ejido Graciano Sánchez, in central Quintana Roo state, in the medium stature semi-evergreen forest (Miranda and Hernández, 1964) receiving approximately 1200 mm mean annual rainfall. The site is classified as dry forest according to Holdridge (1967), which includes everything up to 2000 mm per year. The semi-evergreen forest is the most extensive type on the Yucatan Peninsula and currently covers approximately 25,640 km² in Campeche, Quintana Roo, and Yucatan states. This forest type has previously been described by Olmsted

and Duran (1990), Whigham et al. (1991), White and Darwin (1995), and Olmsted et al. (1999).

Common tree species of this forest type include *Brosimum alicastrum* Sw., *Manilkara zapota* (L.) Royen, *Alseis yucatanensis* Standl., *Pouteria unilocularis* (Donn. Sm.) Baehni, *Drypetes lateriflora* (Sw.) Krug and Urb., *Gymnanthes lucida* Sw., *Sideroxylon foetidissimum* Jacq., *Talisia olivaeformis* Radlk., and *Coccoloba diversifolia* Jacq. Composition and dominance vary latitudinally. Basal area typically ranges from 30 to 45 m² ha⁻¹ and total height from 15 to 25 m, increasing from north to south along an increasing rainfall gradient. Tree species richness varies between 45 and 80 species/ha (Olmsted and Duran, 1990; Whigham et al., 1991).

The study site is located within a large stand of this forest type in La Pantera, Quintana Roo, managed by the Plan Piloto Forestal, a state forest management program, run by rural communities. We were allowed to harvest a 3700 m² portion of forest, which the Plan Piloto Forestal was going to clear for wood storage.

2.2. Biomass measurements

A 0.5 ha forest stand was divided into fifty 10 m × 10 m plots. To assess species composition, basal area and allometry of large trees, every tree >10 cm dbh was identified and its dbh measured. In fifteen 10 m × 10 m plots all individuals with dbh >1 and <10 cm were identified and their dbh measured for composition, basal area and allometry of small trees.

Of the 213 large trees (>10 cm) in 37 plots (3700 m²), 195 individuals were felled. The remaining 18 trees were not felled because the local community planned to sell some of the individual trees. Five hundred and three individuals <10 cm dbh in 10 plots (1000 m²) were also cut. Thus out of 50 small plots, 37 were harvested for large tree biomass and 10 were harvested for small tree biomass.

After the trees were harvested, bole and total heights were measured with a steel tape. The boles were cut into manageable sections, and each section was weighed. A 5 cm thick disk was cut at three different locations along the bole and weighed to the nearest gram, to be later used for dry weight determination. The major branches were also cut and weighed, as were the small twigs and leaves.

Samples were taken from each tree component for dry weight determinations. All data were collected on a per species basis, so that biomass determinations for each species could be made.

Samples were dried to a constant weight in an oven at 55 °C and dry:wet weight ratios were calculated. Total dry weight of each tree's individual compartment (trunk, branches, twigs plus leaves) was determined and the total aboveground dry weight of each

Table 1

Species and basal area in a dry semi-evergreen forest of the Yucatan Peninsula, Mexico^a

Species ^b	<i>n</i>	Basal area (cm ²)
(A) Large trees (>10 cm dbh; plot size = 5000 m ²)		
<i>A. yucatanensis</i> Standl.	29	7867
<i>Astronium graveolens</i> Jacq.	12	5640
<i>B. alicastrum</i> Standl.	38	34733
<i>Croton lundellii</i> Sw.	8	845
<i>Exostema mexicana</i> A. Gray	7	2046
<i>Luehea speciosa</i> Wildl.	6	5961
<i>M. zapota</i> (L.) Royen	31	15336
<i>Pouteria campechiana</i> (Kunth) Baehni	16	5446
<i>P. unilocularis</i> (Donn. Sm.) Baehni	35	5307
<i>S. foetidissimum</i> Jacq.	5	2109
<i>S. mombin</i> Linn.	6	6552
<i>T. alisia olivaeformis</i> Radlk.	11	5185
<i>Trichilia minutiflora</i> Standl.	50	6303
Other species (26)	48	23047
Total	302	126377
Basal area (m ² ha ⁻¹)		25.28
(B) Small trees (<10 cm dbh; plot size = 1500 m ²)		
<i>A. yucatanensis</i> Standl.	12	142
<i>B. alicastrum</i> Standl.	9	112
<i>Croton arboreus</i> Millsp.	22	94
<i>C. lundellii</i> Sw.	14	171
<i>Cydista potosina</i> Loes. ^c	78	601
<i>M. zapota</i> (L.) Royen	27	753
<i>Piper</i> sp. (<i>P. amalago</i> Linn.?)	79	233
<i>P. unilocularis</i> (Donn. Sm.) Baehni	119	2135
<i>T. olivaeformis</i> Radlk.	41	294
<i>T. minutiflora</i> Standl.	329	3789
Other species (49)	105	676
Total	835	9000
Basal area (m ² ha ⁻¹)		6
Overall total basal area (m ² ha ⁻¹)		31.28

^a Includes both harvested and un-cut trees.

^b The source of the species taxonomic authorities is the International Plant Names Index (<http://www.ipni.org>).

^c Vines.

individual tree was computed by summation. The dry weight of the un-cut individuals of both size classes in the 0.5 ha plot was estimated with allometric regression equations, as described below.

2.3. Allometric regression equations

Several allometric regression equations were tested, by using dbh, total height, and trunk height. Use of $\text{dbh}^2 \times \text{total height}$ always produced the highest correlation coefficients. Individual regression equations were derived for the six most abundant species. The other 34 species were grouped, since most species were not represented by enough individuals to derive a separate regression model. A global regression model was derived from the actual weights for all species combined and used to calculate biomass of the remaining 18 large individual trees in the 3700 m² tract that were not cut for the reason explained above. To calculate biomass for the individuals <10 cm dbh, we also calculated allometric regression equations. Individual equations were calculated for the nine most abundant species and a global model was developed for all species combined.

Table 2

Biomass equations derived for the most abundant species at La Pantera, Quintana Roo, Mexico

Species ^a	Regression model ^b		<i>R</i> ²	<i>n</i>
	β_0	β_1		
Large trees (>10 cm dbh) ^c				
<i>A. yucatanensis</i> Standl.		0.0301	0.91	20
<i>B. alicastrum</i> Sw.		0.0336	0.97	17
<i>M. zapota</i> (L.) Royen		0.0447	0.98	20
<i>P. campechiana</i> (Kunth) Baehni		0.0358	0.94	11
<i>P. unilocularis</i> (Donn. Sm.) Baehni		0.0465	0.96	27
<i>T. minutiflora</i> Standl.		0.0465	0.97	37
Small trees (<10 cm dbh)				
<i>A. yucatanensis</i> Standl.	0.0867	0.0429	0.99	9
<i>M. zapota</i> (L.) Royen	0.0034	0.0482	0.89	16
<i>P. unilocularis</i> (Donn. Sm.) Baehni	0.8322	0.0429	0.95	59
<i>T. minutiflora</i> Standl.	0.4125	0.0421	0.96	170
<i>Piper</i> sp.	0.3627	0.0322	0.72	64
<i>T. olivaeformis</i> Radlk.	0.0493	0.0480	0.98	24
<i>C. arboreus</i> Millsp.	0.2385	0.0580	0.99	20
<i>C. lundellii</i> Standl.	0.1780	0.0638	0.92	10
<i>Eugenia</i> sp.	0.4600	0.0370	0.99	7

^a The source of the species taxonomic authorities is the International Plant Names Index (<http://www.ipni.org>).

^b Regression models are of the form $Y = \beta_0 + \beta_1 D^2 \text{TH}$, where *Y* is the biomass (kg dry weight), *D* the dbh (cm), and TH the total height (m).

^c Intercept, β_0 , is set to zero for large trees.

Comparisons with Brown's (1997) tropical dry forest biomass model were done by applying her equation:

$$Y = \exp\{-1.996 + 2.32 \ln(D)\}$$

where *Y* is the biomass (kg) and *D* the dbh (cm), and examining the differences between our measured data and the modeled estimates by species.

3. Results

3.1. Forest composition

We found a total of 39 species among the individual trees with dbh >10 cm, 59 species among the individual trees with dbh <10 cm (Table 1), and a total of 72 different species of trees and lianas in the 5000 m² plot. The basal area of the large trees was 25.28 m² ha⁻¹, while the basal area of the small trees was 6 m² ha⁻¹, totaling 31.28 m² ha⁻¹ (Table 1). In the larger tree category, diameter ranged up to 82.1 cm and height varied from 8 to 30 m. The range in height was 2–10 m in the smaller tree category.

Table 3
Aboveground biomass of trees in two size classes at La Pantera

	<i>n</i>	Biomass (kg dry weight)	Plot size (m ²)	Biomass density (Mg ha ⁻¹)
Large trees (>10 cm dbh)			3700	191.5
Harvested	195	54432		
Calculated	18	16426		
Small trees (<10 cm dbh)			1000	33.5
Harvested	503	3352		
All trees				225

Table 4
Comparisons of actual and calculated (Brown, 1997) biomass of large (10–63 cm dbh) trees at La Pantera

Species ^a	<i>n</i>	Diameter dbh (cm)		Actual biomass (kg)	Calculated biomass ^b (kg)	Difference ^c (%)
		Minimum	Maximum			
<i>Albizia tomentosa</i> Standl.	2	11.3	17.4	249	140	43.8
<i>A. yucatanensis</i> Standl.	20	11.6	29.2	2578	2384	7.5
<i>A. graveolens</i> Jacq.	6	16.5	38.2	2541	1703	33
<i>B. alicastrum</i> Sw.	17	12.8	63.4	14843	9076	38.9
<i>Bursera simarouba</i> (L.) Sarg.	1	18.6	18.6	179	120	32.9
<i>Casearia corymbosa</i> Kunth	3	10.7	14.5	319	162	49.1
<i>Casimiroa edulis</i> S. Watson	1	17.2	17.2	209	100	52.2
<i>Coccoloba acapulcensis</i> Standl.	1	27.4	27.4	287	294	-2.5
<i>C. arboreus</i> Millsp.	1	13.1	13.1	125	53	57.5
<i>C. lundellii</i> Standl.	4	10.5	12.1	316	147	53.5
<i>D. lateriflora</i> (Sw.) Krug and Urb.	3	10.6	11.9	169	114	32.2
<i>E. mexicana</i> A. Gray	3	17.1	24.5	935	497	46.8
<i>Exothea diphylla</i> (Standl.) Lundell	1	17.2	17.2	316	100	68.3
<i>Hippocratea excelsa</i> Kunth	2	13.9	15.9	138	144	-4.9
<i>Laetia thammia</i> L.	2	10.2	21	340	188	44.5
<i>L. speciosa</i> Willd.	5	28.2	45.4	3323	2843	14.5
<i>M. zapota</i> (L.) Royen	20	10	53.3	6663	4434	33.5
<i>Neea choriophylla</i> Standl.	1	15.1	15.1	153	74	51.8
<i>N. psychotrioides</i> Donn. Sm.	3	13.5	28.5	467	458	2
<i>P. campechiana</i> (Kunth) Baehni	11	10.7	25.8	2748	1734	36.9
<i>P. unilocularis</i> (Donn. Sm.) Baehni	27	10.3	24.3	3266	1811	44.6
<i>Protium copal</i> (Schltdl. and Cham.) Engl.	1	10.2	10.2	60	30	50.5
<i>Sabal mauritiforme</i> Griseb. and H. Wendl.	2	21.5	24.4	444	393	11.5
<i>S. foetidissimum</i> Jacq.	4	16.1	34.2	1428	949	33.5
<i>Simarouba glauca</i> Cronquist	1	16.6	16.6	120	92	23
<i>S. mombin</i> Linn.	6	24.4	50.2	3032	3697	-21.9
<i>T. olivaeformis</i> Radlk.	3	12.9	34.1	1872	900	51.9
<i>Thouinia paucidentata</i> Radlk.	2	25	31.7	455	651	-42.9
<i>Trichilia arborea</i> C. DC.	1	17.1	17.1	108	99	9
<i>T. minutiflora</i> Standl.	37	10.2	18.9	3198	1804	43.6
<i>Trophis racemosa</i> Urb.	1	21.2	21.2	231	162	29.7
<i>Vitex gaumeri</i> Greenm.	2	30.5	45.8	1774	1346	24.1
<i>Zuelania guidonia</i> (Sw.) Britton and Millsp.	1	44	44	1546	883	42.9
Total	195			54429	37578	31

^a The source of the species taxonomic authorities is the International Plant Names Index (<http://www.ipni.org>).

^b Equation is $Y = \exp\{-1.996 + 2.32 \ln(D)\}$, where Y is the biomass (kg dry weight) and D the dbh (cm).

^c Percentages are computed in relation to actual weights.

3.2. Biomass estimation and derivation of allometric equations

Based on the dry weight for each individual of each species of the large trees, allometric regression equations derived for the six species, each represented by 11–37 individuals had correlation coefficients of at least 0.91 (Table 2). The biomass for the 195 harvested trees with dbh >10 cm was 54,432 kg (Table 3). The global large tree regression model derived from the actual weights for all species combined was

$$Y = \exp\left\{-2.173 + 0.868 \ln(D^2 \text{ TH}) + \frac{0.0939}{2}\right\},$$

$$R^2 = 0.90$$

where Y is the total dry weight (kg), D the diameter at breast height (cm) and TH the total height (m). The calculated biomass for the 18 un-cut individual trees is 16,426 kg (Table 2). The total biomass in 3700 m² is 70,858 kg or 191.5 Mg ha⁻¹.

The total dry weight of the 503 individuals < 10 cm dbh in the 1000 m² sub-plot was 3352 kg or 33.5 Mg ha⁻¹ (Table 3). Allometric equations were derived for the nine most common species in the same way as with the larger trees (Table 2). The total aboveground tree biomass in this stand of dry semi-evergreen forest is 225 Mg ha⁻¹ (Table 3).

3.3. Other regression models

We also compared the actual dry weight of our harvested plots with biomass calculated with a published equation for dry forests (Brown, 1997), which is based on dbh alone. The dry weight modeled this way for 195 cut trees in 3700 m² at La Pantera is 37,578 kg versus 54,429 kg actual dry weight, an overall difference of 31% (Table 4). The results are represented as totals by species. Some individuals of several species show higher calculated dry weight values than the equivalent real measured weights.

4. Discussion

This is the first biomass study of medium stature semi-evergreen forest on the Yucatan Peninsula employing destructive sampling of a large sample of individual trees (total = 698). The forest composition

and basal area are similar to other forests of this type (Olmsted and Duran, 1984; Whigham et al., 1991) in the same area. However, caution should be employed in generalizing our data from a 0.5 ha plot to this whole forest type.

Our results include only the tree components located aboveground. Others have reported variable root:shoot ratios but, in general, root biomass is approximately 25% of aboveground biomass (Cairns et al., 1997). Our results are applicable to the dry semi-evergreen forest type covering approximately 26 km² of the Yucatan. However, the allometric relationships predicting biomass for this 0.5 ha plot, may be less accurate in wetter forests to the south or drier forests to the north within the same forest type. Their likely accuracy within the broader realm of the world's tropical dry forests, where rainfall varies from 500 to 2000 mm per year, and the species composition is quite different is even less sure.

The aboveground biomass of 191.5 Mg ha⁻¹ for individuals with dbh >10 cm, combined with the biomass for individuals with dbh <10 cm (33.5 Mg ha⁻¹) of aboveground biomass, totals 225 Mg ha⁻¹ (Table 3). The latter is double the aboveground biomass calculated by Cairns et al. (2000) for the semi-evergreen tall/medium forest in the three states of the Yucatan Peninsula (111.2 Mg ha⁻¹), but very similar to their estimate for the state of Veracruz (225.8 Mg ha⁻¹). These forest types and biomass densities are not strictly comparable for several reasons. Cairns et al. (2000) defined a forest class (tall/medium stature *selva*) that included both tall and medium stature semi-evergreen and evergreen species. This would tend to make the biomass differences even greater. However, the primary reason for the discrepancy is that the lower Cairns et al. (2000) biomass estimates are calculated from published biomass regression equations applied to national forest inventory data. The inventory plots were located on an unbiased grid pattern. Thus they included both open and degraded forests along with intact forests like that exemplified by La Pantera. As with forest composition, care must be employed in applying the biomass density of our plot to a larger scale.

The biomass of the small trees (33.5 Mg ha⁻¹) comprises approximately 15% of the total biomass density (225 Mg ha⁻¹) in this forest (Table 3). Although 18 of the 213 trees used to compute the

large tree biomass density (8%) were not harvested, the un-cut trees were of the same species, and approximately within the same size distribution, as the harvested trees. Only one tree, a *Ficus* sp. with a dbh of 82.1 cm, was outside the range of the destructive harvest, and would not significantly change the biomass density estimate.

Separation of the individual trees into two size groups with separate allometric equations may enable calculation of more precise biomass estimates reflecting changes in geometric growth forms as trees age. The use of the species-specific equations (Table 2) for the dominant trees enables accurate estimates of aboveground tree biomass in other mature and successional forests located elsewhere. There is a need for biomass estimates for reliable methods of measuring environmental services such as C sequestration.

Martínez-Irizar (1995) reported biomass densities for 15 different dry forests which range in precipitation from 500 to 1500 mm per year. The aboveground biomass ranges from 23 to 268 Mg ha⁻¹, with 12 of the 15 sites less than 144 Mg ha⁻¹. Her report for the wettest site, Ping Kong, Thailand (1500 mm), similar to our study area, includes values of both 268 and 144 Mg ha⁻¹. Our measured biomass was near the high end of the range reported by Martínez-Irizar (1995). The only other primary data from Mexican dry forest sites were 85 Mg ha⁻¹ in Chamela, Jalisco (Martínez-Irizar et al., 1992) and 63 and 85 Mg ha⁻¹ for two secondary dry deciduous forests on the Yucatan Peninsula (Mizrahi et al., unpublished data). A graph of above-ground biomass and rainfall presented by Martínez-Irizar (1995) works well for the lower rainfall ranges (600–800 mm), but fails above 1000 mm. This suggests that the variability of biomass density in forests receiving between 1000 and 1500 mm annual rainfall is large.

Allometric equations containing both diameter and total height rather than diameter alone, when applied to the most abundant species (Table 2), produced biomass estimates closest to the actual weight and should therefore be used for these species in other biomass studies at other locations. Accuracy may be compromised if our dbh² × total height equation including all species is employed in a similar forest where the diameter distribution is similar, but where the species have shorter relative heights. Soil differences may bring about such reversals (I. Olmsted,

unpublished data). In these situations, a regression model containing only diameters would provide a more accurate biomass estimate.

The importance of intensive biomass studies to provide data for global allometric equations is exemplified by the 31% difference between actual total dry weight of the trees in this study and dry weights calculated with the dry forest allometric equation reported by Brown (1997) (Table 4). There is a tendency for Brown's equation to underestimate above-ground tree biomass. Calculated biomass was less than actual biomass for 29 of the 33 species. Eleven of the 195 total trees, representing all individuals of four species, had lower actual than calculated biomass. In the case of *Spondias mombin* Linn., all five individuals have large diameters, but unusual geometric growth forms. The same situation occurs with individuals of other species where height is not proportional to diameter. Five other species had one or more individual trees that also exhibited this trend.

Brown's equation, originally reported by Brown et al. (1989) is based on 29 trees 5–40 cm dbh in a dry forest in India. The equation we report here for large diameter trees included a total of 195 individual trees 10–63 cm dbh. It is not surprising that biomass estimates from the Brown equation differs from actual biomass because the basis for that equation is from a set of trees of entirely different species growing in different edaphic conditions. Because of the very small number of cases where trees have been destructively harvested and weighed, the Brown equation has been applied outside India, where it was developed. For example, Cairns et al. (2000) used the equation for all dry forests in tropical Mexico. Based on the current research, both the biomass in Mexican tropical dry forests and the loss of biomass C to the atmosphere from conversion of those forests to agricultural uses was likely underestimated. The present research adds to the knowledge of dry tropical tree biomass, and can be combined with Brown's (1997) data for broad applications. At the same time, it should be realized that the best allometric equation is one developed from a destructive harvest of trees in the region of interest.

The allometric equations presented in this paper for the determination of biomass for dry semi-evergreen forests and their individual species may allow land managers to make more informed decisions regarding the harvesting and forestation of land suitable for tree

growth. Wise management practices and resource conservation may be enacted through a consideration of environmental services such as C sequestration. If global C markets become a reality, reliable methods useful for estimation of source/sink potential will be required.

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References

- Brown, S., 1997. Estimating biomass and biomass change of tropical forests. A primer. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Brown, S., Iverson, L.R., 1992. Biomass estimates for tropical forests. *World Res. Rev.* 4, 366–384.
- Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14, 161–187.
- Brown, S., Lugo, A.E., 1984. Biomass of tropical forests: a new estimate based on forest volumes. *Science* 223, 1290–1293.
- Brown, S., Gillespie, A.F.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *For. Sci.* 35, 881–902.
- Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1–11.
- Cairns, M.A., Haggerty, P.K., Alvarez, R., de Jong, B.H.J., Olmsted, I., 2000. Tropical Mexico's recent land-use change: a region's contribution to the global carbon cycle. *Ecol. Appl.* 10, 1426–1441.
- FAO (Food and Agriculture Organization of the United Nations), 1993. Forest resources assessment 1990 tropical countries. FAO Forestry Paper 112. FAO, Rome, Italy.
- Gillespie, A.J.R., Brown, S., Lugo, A.E., 1992. Tropical forest biomass estimation from truncated stand tables. *For. Ecol. Manage.* 48, 69–88.
- Holdridge, L., 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica, 206 pp.
- Martínez-Irizar, A., 1995. Biomass distribution and primary productivity of tropical dry forests. In: Bullock, S., Mooney, H., Medina, E. (Eds.), *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge, pp. 326–345.
- Martínez-Irizar, A., Sarukhan, J., Pérez-Jiménez, A., Rincón, E., Maass, M., Solis-Magallanes, A., Cervantes, L., 1992. Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, Mexico. *J. Trop. Ecol.* 8, 87–96.
- Miranda, F., Hernández, X.E., 1964. Los tipos de vegetación de México y su clasificación. *Bol. Soc. Bot. Mex.* 28, 29–179.
- Mizrahi, A., Ramos-Prado, J.M., Jiménez-Osornio, J., 1997. Composition, structure and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan, Mexico. *For. Ecol. Manage.* 96, 273–282.
- Olmsted, I., Duran, R., 1990. Vegetación de Sian Ka'an. In: Navarro, D., Robinson, J. (Eds.), *Diversidad Biológica en Sian Ka'an, Quintana Roo, Mexico*. Program for Studies in Tropical Conservation, University of Florida, Gainesville, FL, USA.
- Olmsted, I., Gonzalez-Iturbe, J.-A., Duran, G.R., Granados, C.J., Tun, D.F., 1999. Vegetación de la Península de Yucatán. Chapter 3 in *Procesos territoriales de Yucatán*. Universidad Autónoma de Yucatan, Merida, Mexico.
- Olson, J.F., Watts, J.A., Allison, L.J., 1983. Carbon in live vegetation of major world ecosystems. Report ORNI-5862, ESD Publication Number 1997. Oak Ridge National Laboratory, Oak Ridge, TN, USA.
- Turner, D.P., Koerper, G.J., Harmon, M.E., Lee, J.J., 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.* 5, 421–436.
- Whigham, D., Olmsted, I., Cabrera Cano, E., Harmon, M.E., 1991. The impact of hurricane Gilbert on trees, litterfall and wood debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23, 434–441.
- White, D., Darwin, S.P., 1995. Woody vegetation of tropical lowland deciduous forests and Mayan ruins in the north-central Yucatan Peninsula, Mexico. *Tulane Stud. Zool. Bot.* 30, 1–25.