Allometric equations for tree species and carbon stocks for forests of northwestern Mexico

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ABSTRACT

Allometric equations were developed and applied to forest inventory data to estimate biomass and carbon stocks for temperate species and forests of Durango and Chihuahua and for tropical dry forests of Sinaloa, Mexico. A total of 872 trees were harvested and dissected into their component parts: leaves and branches, boles, and coarse roots. Coarse roots of 40 temperate trees ranging in diameter at breast height (DBH) from 6.0 to 52.9 cm were excavated in their entirety (i.e., >0.5 cm diameter). The species sampled (number of trees) in tropical dry forests (39) were *Lysiloma divaricata* (Jacq) Macbr. (10), *Haematoxylon brasiletto* Karst. (10), *Cochlospermum vitifolium* (Wild.) (5), *Ceiba acuminata* (S. Watson) Rose (5), *Bursera penicillata* (*B. inopinnata*) (5), and *Jatropha angustifolia* Mull. Arg. (4) and in temperate forests (833) were *Quercus* spp. (118) (*Q. rugosa* Neé, 15, *Quercus sideroxylla* Humb. & Bonpl, 51, *Quercus* spp., 52), *Pinus herrerae* Martinez 1940 (19), *Pinus oocarpa* Schiede ex Schlectendal 1838 (31), *Pinus engelmannii* Carriere 1854 (7), *Psudotsuga menziesii* (Mirb.) Franco (19), *Pinus leiophylla* Schiede ex Schlectendal et Chamisso 1831 (27), *Pinus teocote* Schiede ex Schlectendal et Chamisso (55), *Pinus ayacahuite* Ehrenb. ex Schltdl. (58), *Pinus cooperi* Blanco (48), *Pinus durangensis* Martinez 1942 (385), and *Pinus arizonica* Engelmann 1879 (66). Allometric equations having only DBH as an independent variable were developed for each component of each species. Since *Pinus herrerae*, *Pinus engelmannii*, *Pinus oocarpa* and *Pseudotsuga menziesii* had a small number of trees, an individual allometric equation was developed for these species. We used non-linear regression to fit parameters of the typical allometric power equation. The resulting 31 equations (10 species or groups of species, three biomass components; bole, branch and leaves, and total aerial; and the generalized equation for coarse roots) fit the data well and enable the user to predict biomass by component for each of the 10 different groups of species or each of six temperate species. A single allometric equation that incorporates the basic specific gravity for aboveground biomass of all temperate tree species also fit the data well, and this equation provides both the detail and the accuracy supplied by species-specific, plant-part-specific equations. Biomass equations coupled with forest inventory data for temperate (637 circular, 1/10 ha plots) and tropical dry forests (166 20 m × 20 m-quadrats) of northwestern Mexico predict a mean (confidence intervals) of 130 Mg ha^{-1} (4.2 Mg ha^{-1}) and 73 Mg ha^{-1} (7.1 Mg ha^{-1}) for total tree and total aboveground biomass, respectively. Large sample sizes and the economic and ecological importance of the species studied make this data set uniquely useful for biomass estimations and for understanding the inherent heterogeneity of tree structure in dynamic tropical and temperate environments of northwestern Mexico.

1. Introduction

Estimates of tree biomass are useful in assessing forest structure and condition (Chave et al., 2003; Houghton and Goodale, 2004); forest productivity, carbon stocks and fluxes based on sequential biomass measurements (Clark et al., 2001); and sequestration of carbon in biomass components, including wood, leaves, and roots; as well as being a useful indicator of site productivity.

Several generalized biomass prediction equations have been developed for tropical species (Brown et al., 1989; Chambers et al., 2001; Chave et al., 2005; Overman et al., 1994). For temperate species, Ter-Mikaelian and Korzukhin (1997) reported a list of biomass equations for 66 North American tree species. However, single species and mixtures of species differ in allometry, wood density, and architecture, all of which can affect the relationship between the measurements taken during forest inventories and the biomass of individual trees (Chave et al., 2003). Therefore,

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biomass equations are required for other forest ecosystems where little is known and there is a great need for the development of environmental projects to conserve native forests. Equations developed from single species and from mixtures of species yield useful estimates for specific sites and for large-scale global and regional comparisons. These two types of equations are important for forest inventory data to which single or mixed-species equations are often applied.

In cases where species-specific information is available, equations tailored to estimate biomass of the particular species can provide more accurate estimates of biomass (Litton and Kauffman, 2008). This situation typically arises in cases of plantations of high-value tree species or when precise estimates are needed for research or environmental management. In natural forests, equations must incorporate a variety of species to provide accurate biomass estimates.

We developed allometric equations for 10 species of temperate and tropical dry forests regarding branches and leaves, boles, and roots, taking advantage of measurements made during an intensive study of carbon sequestration in 19 forestry communal lands (ejidos) of northwestern Mexico. Sampled trees spanned a wide range of sizes and were of the largest sizes attainable by the species. These samples are typical of today's native forests grown in the Sierra Madre Occidental mountain range of Durango and Chihuahua and of the tropical dry forests of the lowlands of the Pacific Ocean. We developed allometric equations for each component, as each harvested tree was dissected into various biomass components (branches and leaves, bole, total above-ground, and roots). We then applied the equations to forest inventory data (637 plots of temperate forests and 166 quadrats of dry tropical forests) to estimate biomass and carbon stocks. The economic and ecological value of the species studied, the uniquely large sample sizes, the breakdown of each species into morpho-logical components, and the application to forest inventory data make this a rich data set that can provide insights into biomass allocation and carbon stocks of temperate and tropical trees and forests in northwestern Mexico.

2. Materials and methods

2.1. Study site

This study was conducted at the ejidos of Chihuahua (Papajichi, Guachochi, and Caborachi), Durango (El Tarahumar, El Tule, La Soledad, El Negro, Altares, Valle de Topia, San Miguel, Salto de Camellones, Milpas, Tambores, San Manuel de Villa Corona, San Luis de Villa Corona, San Bartolo, and Santiago Teneraca) and Sinaloa (San Francisco Javier de Tineaquis and Vado Hondo). The ejidos of Durango and Chihuahua are located in the temperate pine–oak forests of the Sierra Madre Occidental mountain range, where the mean annual temperature and rainfall are approxi-mately 12 °C and 900 mm, respectively. The ejidos of Sinaloa are located in the dry tropical forest of the lowlands of the Pacific Ocean with a mean annual temperature and rainfall of 21 °C and 700 mm, respectively. Soils in upland sites are characterized by Litosols and Regosols; and Vertisols in the lowlands of the Pacific Ocean.

2.2. Species

The research project comprised taper, volume and biomass measurements of a large number of temperate trees. For this report, 19 tree species were chosen because they spanned a broad range of phenological and physiological traits, and were species known to distribute well in both the tropical dry forests of the

lowlands of the Pacific Ocean in northwestern Mexico and in temperate pine–oak forests of the Sierra Madre Occidental mountain range of northern Mexico. All sampled species are native to the studied forests, and all are species of economic importance, harvested for industrial timber and other secondary forest products.

2.3. Tropical dry forests

Tropical dry forests in Mexico can be found from Baja California Norte to Chiapas on the eastern coast of the country. On the Gulf of Mexico side it grows from Tamaulipas to Yucatan. The study area was located in the Sinaloan dry forests, which cover an area of 29,900 square miles (77,500 km^2) and stretch through three Mexican states (Sonora, Sinaloa and Nayarit) from the base of the Sierra Madre Occidental Mountains west to the Pacific Ocean. The climate of this area is subtropical subhumid with a long dry season, where distribute the dry forest trees and columnar cacti, including the kapok tree, quiebrocha, and desert fern. Common species according to a forest inventory conducted on the two studied ejidos are: *Lysiloma divaricata*, *Haematoxylon brasiletto*, *Bursera penicillatum*, *Erythrina guatemalensis*, *Guazuma ulmifolia*, *Ipomoea arborescens*, *Ceiba acuminta*, *Pithecellobium mangense*, and *Rubus palmeri*. Of these common species, we selected only six with 39 trees for harvesting and biomass measurements.

2.4. Temperate pine–oak forests

The Sierra Madre Occidental of northwestern Mexico boasts some of the richest biodiversity anywhere in North America, and contains about two thirds of the standing timber in Mexico (http://www.worldwildlife.org/wildworld/profiles/terrestrial/na/na0302_full.html). Twenty-three different species of pine and about 200 species of oak reside within the Sierra Madre Occidental pine–oak forests ecoregion. Many distinctive species have evolved there as a result of the landforms, altitude, temperature and rainfall. Extensive areas of pine–oak forests occur along the eastern side of the continental divide in western Chihuahua. Along the western slope of the Sierra Madre Occidental, the climate is generally somewhat wetter with presumably milder winter temperatures, resulting in a more diverse flora with more tropical elements including Apache pine (*Pinus engelmannii*), Durango pine (*P. durangensis*), egg-cone pine (*P. oocarpa*), pino chino (*P. herrerae*), and Mexican tropical-montane oaks. Pine–oak forests are con-tinuous with oak woodlands at lower elevations. This ecosystem is included within the concept of the Madrean Evergreen Woodland (Brown, 1994), and the pine forest has been called the Madrean Montane Conifer Forest (Brown, 1994). At higher elevations within the pine–oak zones, the pines become increasingly conspicuous and the tree density increases. In Chihuahua, the pine forest is characteristically dominated by one species of pine, usually Arizona pine (*Pinus ponderosa* var. *arizonica*) with scattered individuals or small groups of oaks, especially Gambel oak (*Q. gambelii*) and net-leaf oak (*Q. rugosa*). In Durango, *P. cooperi* Ornelasi dominates the overstory and *Q. sideroxyla* the understory of most pine forests at higher elevations.

2.5. Samples

Using a diameter distribution for the forest inventory of 1997 for several ejidos of the State of Durango, Mexico, trees were selected proportionally per diameter class until completing approximately 50 trees per ejido. Diameter at breast height was recorded using diameter tapes on standing trees. Trees were felled and diameters were measured at the base, 0.5, 1.0, 1.3, and 2.0 m

Table 1
Sample size and range of diameters of trees harvested to determine stature–biomass relationships.

Species or groups of species	N	Diameter at breast height (cm)		Dry weight range (kg)	
		Minimum	Maximum	Minimum	Maximum
Tropical dry forest	39	5.2	32.6	0.6	469.4
Other spp. (*P. oocarpa, P. engelmannii, P. menziesii, P. herrerae*)	81	8.4	49.8	17.4	2371.2
Pinus leiophylla	27	9.6	34.8	16.7	520.2
Pinua teocote	56	7.3	41.2	18.6	1579.3
Pinus ayacahuite	58	5.7	49.2	6.7	1439.3
Pinus cooperi	49	8.2	57.4	18.4	1970.7
Quercus spp.	118	7.3	62.5	14.6	2806.7
Pinus durangensis	384	6.2	57.2	12.4	2839.7
Pinus arizonica	66	10.0	45.0	14.9	922.4
Roots of temperate pine species	40	6.0	52.9	0.4	252.4
All pine species	721	5.7	57.4	6.7	2839.7

and every meter thereafter up to top height. Eight-hundred seventy seven trees were harvested for biomass determination: 700 *Pinus* spp., 21 *Pseudotsuga menziesii*, 118 *Quercus* spp., and 39 trees comprising 6 tree species of the tropical dry forest (Table 1). Of the pine and oak trees harvested, 40 of them were excavated to collect coarse roots and to develop the equation for coarse roots using DBH as the single predictor variable. *Pseudotsuga menziesii* trees were lumped together with pine species (*P. oocarpa, P. engelmannii,* and *P. herrerae*) that have a small number of individuals to develop one equation for the group of trees called other spp. A single equation for all tropical dry forest trees was also developed.

The diameter of each species harvested surpassed 5.2 cm and the largest measured was 62.5 cm (*Quercus sideroxylla*) (Table 1). Diameters were recorded to 0.1 cm every meter from the base of the stem to the tip using diameter tapes. Top height was recorded to 0.1 m and measured directly on the main stem after trees were felled. Harvested trees were dissected into their component parts. At a minimum, this comprised leaves and branches together, bole, and roots. Boles were logged to minimum commercial length (2.50 m) for further commercial use. All leaves and branches, logs, and roots were fresh weighted separately per tree. The root systems of all 40 temperate trees were harvested manually in their entirety and separated into diameter size classes. The total fresh weight of each component was obtained in the field using electronic balances and recorded to 1 g for material weighing less than 5 kg or to 10 g for heavier material. Samples of each component of each tree were fresh weighted and oven-dried (to constant weight at 70 °C). Dry weights were recorded to 0.1 g. Dry to fresh weight ratios were developed for each sample of each component and multiplied by the fresh weight of the biomass component to calculate dry biomass.

Prediction equations fitted inventory data sets to estimate biomass and carbon stocks at the stand scale. For temperate, upland forests of the Sierra Madre Occidental mountain range we used data for 637 circular, 1/10 ha, plots distributed in 24 different properties; 20 ejidos and 4 private properties to calculate bole, branch and foliage, roots and total tree biomass and carbon stock. For tropical dry forests, we used 166 quadrats, 20 m × 20 m distributed in two ejidos near Cosalá, Sinaloa, Mexico to estimate bole, branch and foliage and total aboveground biomass and carbon stocks in aboveground biomass.

2.6. Data analysis

Data analyses were generated using SAS software (SAS, 2000). When analyzing the data, we first examined scatter plots of biomass components and diameter at breast height (DBH). In the case of suspected erroneous values, we reconfirmed field and laboratory data and all calculations. If correct, those data remained in the data set at least temporarily.

We fit the standard form of the allometric equation: $y_i = a(\text{DBH})^b$, where y_i = biomass of tree component i, DBH is the diameter at breast height, and a and b are statistical parameters. We also fitted the allometric equation $y = a(\text{DBH})^{b1}b2^p$, where p: basic specific gravity (g cm^{-3}) for all temperate pine–oak species. We then examined the fit of the data to the equation and reviewed for possible data-recording errors, including any data point whose studentized residual (i.e., the ratio of the residual to its standard error (SAS, 2000)) exceeded ±3 Cook's D. In almost all cases, after checking the field data, those data points were declared outliers and excluded from further analysis. After eliminating outliers, we again calculated the equation's parameters.

We first calculated the scaling factors for two sets of equations for each component of each species. Slopes and intercepts of all relationships were determined, as were the significance of differences among them using PROC NLIN (SAS, 2000). This method provides the slope and intercept parameters and does not require a correction factor to account for the presence of large biomass data used when log transforming the data.

3. Results

The allometric equations generally fit the data well, and in most cases more than 67% of the observed variation in biomass was explained by diameter at breast height (Table 2). The total variance explained by the models was an average (± standard deviation) 89% (± 8.8%). All equations were highly significant ($p < 0.0001$) for both scaling parameters, a and b. The value of the standard error of the mean, Sx, is in the range of most allometric equations, between 15% and 40% of the mean. In general, the allometric equations for branches and leaves exhibited a large variation, having large values for the Sx and small values for the r^2.

The a and b values vary among the species and biomass components, as was observed early by Baskerville (1965) and later by Zianis and Mencuccini (2004). According to the model proposed by West et al. (1997), D is related to M through $D < M^{3/8}$, indicating that the scaling exponent b in the allometric equation equals 2.67 (see also Enquist et al. (1998)). The average (± confidence interval) for our 31 equations was 2.3089 (±0.1082), indicating that it is statistically different from the theoretical average (2.67). This finding is also consistent with the observations of Zianis and Mencuccini (2004), who recorded an average b value of 2.3679 for 279 biomass studies. Thus, it is supported that the potentiality of fractal geometry has not been fully investigated; since the empirical value provides better biomass estimates, further research is necessary to reveal the value of fractal geometry in forest biomass studies.

Table 2
Biomass equations for temperate and tropical species and groups of species.

Species and groups of species	Biomass component	Statistical parameters			
		a	B	Sx	r^2
Tropical dry forests	Bole	0.5825	1.6178	28.22	0.85
	Branch and leaves	0.0433	2.3929	30.63	0.81
	Total aboveground	0.3700	1.9600	52.41	0.85
Other species (P. herrerae,	Bole	0.0348	2.5893	72.86	0.92
P. engelmannii, P. oocarpa, P. menziensii)	Branch and leaves	0.2883	1.7343	58.85	0.72
	Total aboveground	0.1354	2.3033	83.71	0.94
Pinus leiophylla	Bole	0.1855	2.1017	44.99	0.92
	Branch and leaves	0.0255	2.5507	30.33	0.91
	Total aboveground	0.1751	2.2629	67.17	0.93
Pinus teocote	Bole	0.0274	2.6928	33.60	0.97
	Branch and leaves	0.4452	1.7682	46.83	0.89
	Total aboveground	0.2057	2.2583	71.55	0.96
Pinus ayacahuite	Bole	0.0690	2.4515	46.82	0.97
	Branch and leaves	0.6437	1.6020	34.25	0.92
	Total aboveground	0.2893	2.1569	62.39	0.97
Pinus cooperi	Bole	0.1899	2.2270	104.89	0.96
	Branch and leaves	0.0254	2.4828	124.39	0.68
	Total aboveground	0.2018	2.2907	176.70	0.94
Quercus spp.	Bole	0.0768	2.4416	102.94	0.95
	Branch and leaves	0.0202	2.6480	100.30	0.86
	Total aboveground	0.0890	2.5226	156.96	0.95
Pinus durangensis	Bole	0.1314	2.2815	118.78	0.87
	Branch and leaves	0.0175	2.5739	84.92	0.67
	Total aboveground	0.1382	2.3573	139.21	0.91
Pinus arizonica	Bole	0.0992	2.2674	35.31	0.96
	Branch and leaves	0.0063	2.8284	30.76	0.87
	Total aboveground	0.0819	2.4293	43.65	0.97
All Pine species	Bole	0.0726	2.4459	105.00	0.89
	Branch and leaves	0.0565	2.2729	84.32	0.69
	Total aboveground	0.1229	2.3964	131.80	0.91
Coarse roots		0.0051	2.6680	15.59	0.94

All equations are in the form $y_i = a(\text{DBH})^b$. Scaling factors a and b differ significantly from 0 ($p < 0.01$). Sx is the root mean square error (kg). The r^2 is the coefficient of determination calculated from the regression sum of squares and the total uncorrected sum of squares.

Parameters a and b are well related by a power equation: $a = 5.1385b^{-4.4857}$; $r^2 = 0.72$, in agreement with the equation of $a = 7.0281b^{-4.7558}$ when M is expressed in kg and D in cm reported for 277 compiled biomass studies by Zianis and Mencuccini (2004). Three similar equations were reported by Pilli et al. (2006) for young, juvenile and mature trees, showing the consistency of our biomass equations and the relationship between a and b. These regression equations are consistent, although, the statistical parameters of our equation were calculated using non-linear regression. Linear regression is the common statistical technique for calculating parameters of the log transformed biomass and DBH data.

The groups of species differ in allometric relationships, though more so with boles than branches and leaves (Fig. 1). The regression lines for boles reflect a substantial amount of inherent variation especially among large trees, resulting in few significant ($p < 0.01$) differences in slope among regression lines; species of pine–oak forests, Pinus and Quercus, have a steeper slope than species of the tropical dry forest. A smaller range of measured diameters (5.2–32.6 cm) in tropical dry forests in contrast to pines (5.7–57.4 cm) and oaks (7.3–62.5 cm) may explain the smaller slope. Other sources of variation could be due to determining the end of the bole. Indeed most species of tropical dry forests are multi-stemmed in nature and allometry is different. For the relationships between biomass of branches and foliage and DBH, the slopes are similar among groups of species.

The residuals for the individual components of any particular species might be correlated. To report an estimate of the error associated with calculation of whole-tree biomass determined by summing the values derived from equations for individual components, it would have been necessary to employ a procedure such as non-linear seemingly unrelated regression (NSUR) (Parresol, 1999, 2001). Because we developed an equation for the pine–oak ecosystem incorporating the basic specific gravity of the studied species, we wished to be consistent with the technique employed to estimate scaling factors. An approach such as NSUR was not feasible for the general allometric equation.

The forest inventory coupled with the generalized biomass prediction equations for conifers and broadleaf trees predict a mean (confidence intervals) of 130 Mg ha^{-1} (4.2 Mg ha^{-1}) in tree biomass density for all 637 sample plots inventoried in temperate forests of south central Durango. Of this, 62%, 29% and 9% belong to boles, branches and foliage and coarse roots, respectively. Tree biomass of conifers explains 62% and broadleaf trees the remaining 38% (Fig. 2) of the total biomass in temperate forests. Using the carbon factor of 0.50, upland, temperate forests have a mean carbon stock of 65 Mg ha^{-1} (2.1 Mg ha^{-1}) in standing trees, including coarse roots.

The mean (confidence intervals) aboveground biomass stock for tropical dry forests was 73 Mg ha^{-1} (7.1 Mg ha^{-1}), of which
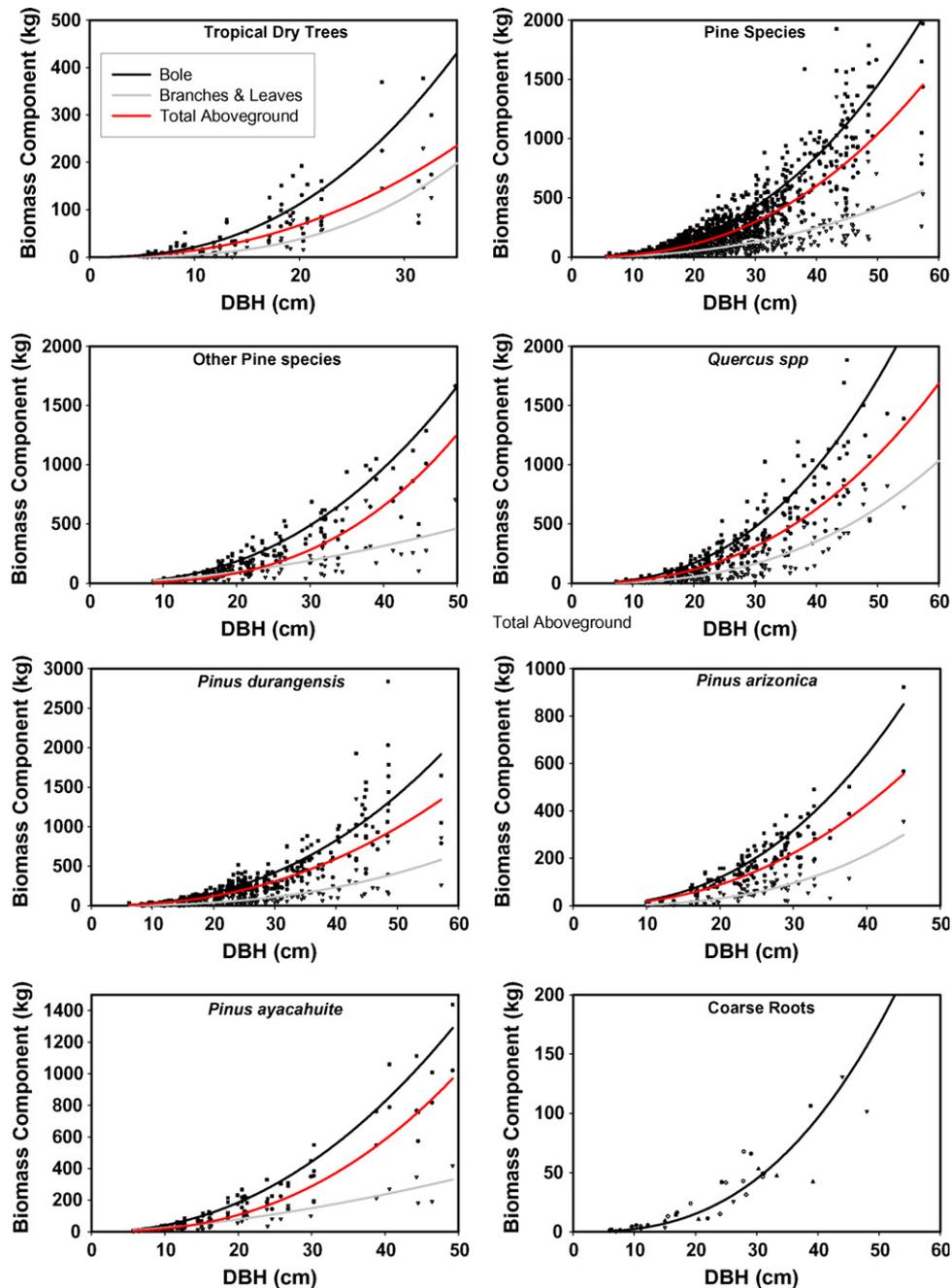
Fig. 1. Allometry of foliage and branches, boles, total aboveground and coarse roots for temperate and tropical dry species of northwestern Mexico.

branches and foliage accounted for by 51% and the remaining 49% by boles (Fig. 3). Tropical dry forests of eastern Sinaloa, Mexico have a mean carbon stock in aboveground standing trees of 36.5 Mg ha^{-1} (3.5 Mg ha^{-1}).

4. Discussion

The large sample size, coupled with a large variation in diameter values, provides precise estimates of biomass as well as a degree of insight into the dynamics of tree allometry that would not have been forthcoming had we sampled fewer numbers of larger trees. Species-specific equations are very useful in assessing biomass estimates needed for accurate determination of linked factors such as carbon and nutrient storage, or for evaluation of the performance of species such as those in this study.

The allometric equation is a satisfactory predictor of biomass since the total variation explained by the relationships was above 67%, with an average of ($\pm$confidence interval) 89% ($\pm$0.03%). The relationship is much stronger for trees with larger biomass weights (i.e., those having large biomass amounts in the bole or total aboveground biomass; $r^2 > 0.94$). The branch and foliage biomass components are always difficult to predict with the precision of bole or total aboveground biomass. Competition for light between neighboring trees may account for some of this variation; trees growing under strong competition and attaining a dominant position recorded small branch and leaf biomass. On the other hand, trees growing in open spaces tended to have widespread crowns and large biomass in branches and leaves in contrast to that of the bole.

The ability to predict the biomass of large woody components such as boles and total aboveground biomass tends to be more

Table 3

Basic specific gravity values reported for pines and oaks of Durango and Chihuahua, Mexico.

Species	Basic specific gravity (g cm^{-3})	Author
Pinus arizonica	0.43	Echenique-Manriquez and Plumtre (1994)
Pinus durangensis	0.46	Echenique-Manriquez and Plumtre (1994)
Pinus cooperi	0.39	Echenique-Manriquez and Plumtre (1994)
Pinus ayacahuite	0.42	Fuentes-Salinas (1995)
Pinus teocote	0.51	Fuentes-Salinas (1995)
Pinus leiophylla	0.44	Echenique-Manriquez and Plumtre (1994)
Pinus herrerae	0.44	Mean Pines Durango
Pinus engelmannii	0.44	Mean Pines Durango
Pinus oocarpa	0.55	Martin (1984)
Pseudotsuga menziesii	0.444	USDA FS (1984)
Quercus sideroxyla	0.63	Nájera-Luna et al. (in press)
Quercus spp.	0.64	Mean Quercus for Durango
Quercus rugosa	0.60	Fuentes-Salinas (1995)

stable than that of smaller, shorter-lived components such as branches and leaves. Branch and foliage biomass is susceptible to weather, herbivores, and inter-plant competition. In densely spaced forests, it is likely that intraspecific competition influences crown geometry and therefore the heterogeneity of branch and leaf biomass from tree to tree. Because of the unusually large number of trees sampled, the equations are indicative of the degree of variation to be anticipated among conspecific trees; breakage, reiteration, herbivory, competition, and a number of other factors lead to the irregularity that is typical of species such as these.

The single metric most commonly used for tree allometry is diameter, as is evident in the review (65 species) of Ter-Mikaelian and Korzukhin (1997) and the synthesis (279 equations) compiled by Zianis and Mencuccini (2004). Statistical fits are generally useful, enabling one to use locally developed equations with confidence for the stands from which they were derived. Tree height is more tedious to measure and may not explain more of the variance at the site where the data originated, but its incorporation has the advantage of increasing potential applicability of the equation to different sites (Ketterings et al., 2001). However, to be consistent with the scientific literature and with the development of simple models, the allometric equations employed DBH as the single predictor variable.

Several biomass equations have been published relating tree biomass to diameter or diameter and height. Almost all of these relationships, whether intended for application to a particular species, mixed-composition forests, specific sites, biogeographical regions, or climate-related biomes, are based the allometric equation. Use of the allometric equation is appealing because of its grounding in theory (Niklas, 1994; West et al., 1997), but its application to groups of species is problematic for two reasons: first, wood density changes with the species, and second, wood density changes within the species following the bole length and inside the stem. Changes in wood basic specific gravity with bole length, and between woody components (softwood and hardwood) incorporate an additional source of variation, obfuscate form–function relationships, and change with tree age, as is clear from data reported immediately above.

For regionally comparable estimates of biomass, an equation that incorporates terms for those aspects of forest structure that vary significantly at regional scales is required. For this type of comparison, other factors in addition to tree diameter may also be important. Wood specific gravity varies widely between tropical forest tree species and is closely related to differences in diameter growth rates (Baker et al., 2004; Chave et al., 2001, 2003). This

component also varies notoriously in temperate pine–oak forests since there is an important tree diversity and therefore in wood specific gravity. Therefore, a single equation for all temperate species that incorporates the wood basic specific gravity was developed for total aboveground biomass. The basic specific gravity values incorporated into the allometric equation for all temperate pine–oak species are reported in Table 3.

The equation (with the standard errors) that represents the lines in Fig. 4 to predict total aboveground biomass with the inclusion of specific gravity was: $Bt = 0.0752(0.0108)$ $D^{2.4448(0.0376)} \times 2.0331(0.2348)^p$; where Bt = total aboveground biomass, D = diameter at breast height (1.3 m), and p = wood basic specific gravity. The standard error was 136 kg (r^2 = 0.93). This equation explains that as the wood basic density increases, so does the total aboveground biomass (Fig. 4).

The equation reported in here is consistent to biomass functions that include wood basic specific gravity, since most investigators reports equations of the form: $(p/pw) \times \exp(-1.839 + 2.116 \ln D)$ (Hughes et al., 1999); $(p_i/0.58) \exp(-2.00 + 2.42 \ln D)$ (Chave et al., 2001); $(p_i/0.67) \exp(0.33(\ln D) + 0.933 \ln(D)^2 - 0.122 \ln(D)^3 - 0.37)$ (Chambers et al., 2001); and $(p/0.60) \times \exp(-3.742 + 3.450 \ln D - 0.148 \ln(D)^2)$ (Chave et al., 2003); where p_i = wood basic specific gravity of the species i and pw = mean basic specific gravity. These allometric equations are useful to calculate the biomass of forests with a complex diversity structure in which exist tree species with a wide range of weights with the same volume because of changes in the basic specific gravity. Since the basic specific gravity is a function of the stem length, this source of variation is likely to be incorporated in future allometric equations.

Roots sampled by digging soil pits are commonly used to estimate root mass, but this approach misses the mass of fine roots and needs to be sampled separately (Resh et al., 2003). The applicability of the equations we developed (Table 2) is restricted to a root biomass component with dimensions of >0.5 cm in diameter. This data makes our estimates of total aboveground and branch and foliage to-belowground biomass ratios (ABR) to be on the average (±confidence intervals) of 10.89 (±1.89) and 3.54 (±0.67). However, both ABR values tended to diminish to approximately 8 and 2, respectively, in trees with a large diameter at breast height. Our first mean ABR value is close to the value reported for a 73-year-old Scots pine stand (Chun-Wang et al., 2003), as well as to values between 12 and 20 reported for tropical trees of approximately 30 cm DBH found in Costa Rica.
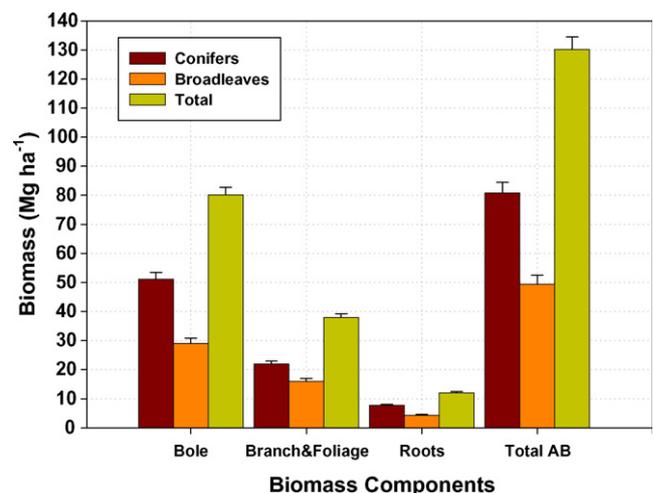

Fig. 2. Biomass stocks by components in upland temperate forests of south-central Durango, Mexico (n = 637 inventory plots).
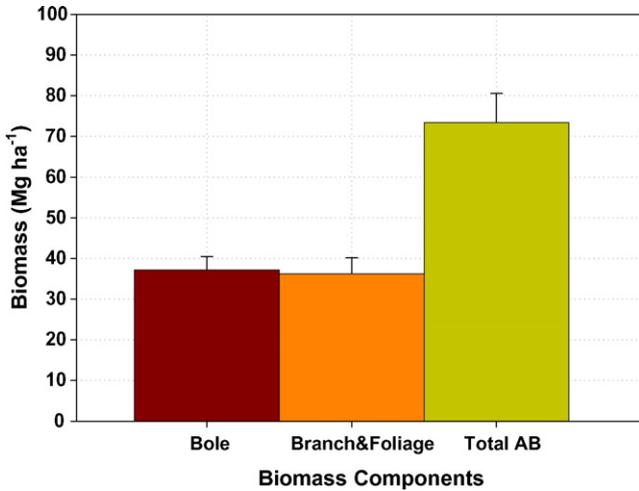
Fig. 3. Biomass stocks by components in tropical dry forests of eastern Sinaloa, Mexico ($n = 166$ inventory quadrats).

Fig. 5. Comparisons of equations developed to estimate aboveground biomass for tropical dry trees.

Comparisons of the biomass equation for total aboveground biomass for the tropical dry forests of eastern Sinaloa with other equations developed for other tropical dry forests (Brandeis et al., 2006; Brown, 1997; Litton et al., 2006; Litton and Kauffman, 2008; Martínez-Yrízar et al., 1996) produced mixed results (Fig. 3). Total aboveground biomass estimates are similar for trees with diameter of less than 25 cm for equations developed in this study, by Brown (1997) for tropical dry forests worldwide; by Litton et al. (2006) for *Psydrax odorata* of Hawaii, and by Martínez-Yrízar et al. (1996) for tropical dry forests of Jalisco, Mexico. For trees with larger diameters, the biomass equation developed in this study deviated least to biomass equations reported by Brown (1997) and by Litton et al. (2006) for *Psydrax odorata* in tropical dry forests of Hawaii (Fig. 5).

Mean aboveground biomass and carbon stock reported in this study for temperate forests is a bit larger than figures reported for temperate forests of the state of Nuevo Leon, Mexico. Using 88 forest inventory plots, Návar (submitted for publication) estimated a mean aboveground biomass and carbon density (confidence intervals) of 74.2 Mg ha^{-1} and 37.1 Mg ha^{-1} (11.9 Mg ha^{-1} and 5.9 Mg ha^{-1}), with a large spatial variation of 60 Mg ha^{-1} and 30 Mg ha^{-1} for the standard deviations of biomass and carbon density, respectively. Jaramillo et al. (2003) recorded carbon stocks
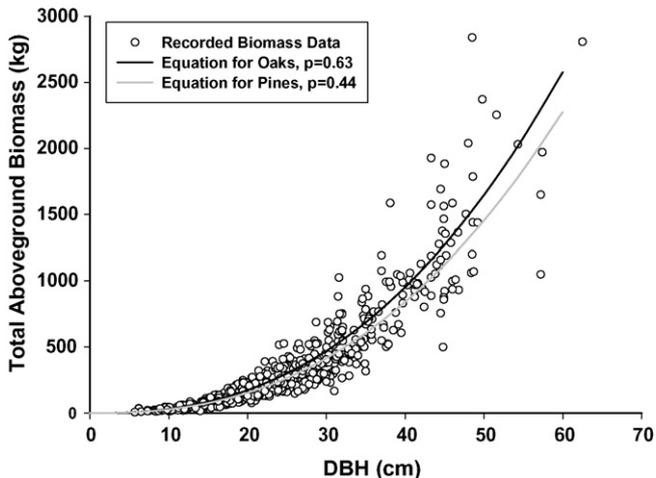
in aboveground biomass of 47–62 Mg ha^{-1} for a temperate forest in Central Mexico. Temperate forests of the western Sierra Madre mountain range of northern Mexico appear to have larger biomass and carbon stocks than other temperate forest of the country. In fact, the State of Durango is considered the main timber reservoir of Mexico.

Biomass and carbon stocks in aboveground components are similar to figures reported for other the tropical dry forests of southern Mexico. Castellanos et al. (1991) reported biomass and carbon stocks of the order of 73.6 Mg ha^{-1} and 33 Mg ha^{-1}, respectively for the tropical dry forest of Jalisco, Mexico. Hughes et al. (2000) recorded 88 Mg ha^{-1} and 44 Mg ha^{-1} for biomass and carbon stock in aboveground components of tropical dry forests of southern Mexico. In tropical dry forests of the Yucatan Peninsula, total carbon stocks in aboveground tree biomass was estimated to be 112.5 Mg ha^{-1}, and was dominated (85%) by the biomass of the large trees (Cairns et al., 2003).

Fig. 4. The relationship between total aboveground biomass and DBH with the inclusion of the basic specific gravity term.

References

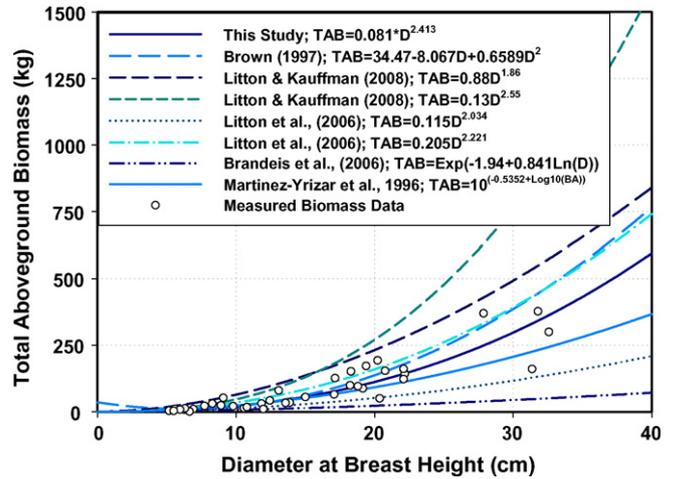Baker, T.R., Phillips, O.L., Malhi, Y., Almeidas, S., Arroyo, L., Di Fiori, A., Erwin, T., Keleen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudos, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Natalina, J., Silva, M., Martínez, R.V., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10, 545–562.

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