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Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data

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ABSTRACT. This paper contains a strategy for estimating total aboveground biomass of tropical forests. We developed regression equations to estimate aboveground biomass of individual trees as a function of diameter at breast height, total height, wood density, and Holdridge life zone (*sensu* Holdridge 1967). The regressions are applied to some 5,300 trees from 43 independent sample plots, and 101 stand tables from large-scale forest inventories in four countries, to estimate commercial and total aboveground biomass per unit area by forest type, and to estimate expansion factors defined as the ratio of aboveground to commercial biomass. The quadratic stand diameter (QSD, i.e., the diameter of a tree of average basal area) in a given forest stand influences the magnitude of the expansion factor. Stands of small trees have large expansion factors (up to 6.4), and as QSD increases, the expansion factor decreases to a constant value (about 1.75). For undisturbed forests in moist, moist transition to dry, and dry life zones respectively, the expansion factors for total aboveground biomass were 1.74, 1.95, and 1.57 respectively. For undisturbed, logged, and nonproductive forest categories used by the FAO to report global commercial wood volume data, we estimated expansion factors of 1.75, 1.90, and 2.00 respectively. Applying these factors to FAO data results in a 28 to 47% increase in previous volume-derived estimates of tropical forest biomass. However, estimates of tropical forest biomass based on small destructive samples continue to be high relative to estimates based on volume data. FOR. SCI. 35(4):881–902.

ADDITIONAL KEY WORDS. Global carbon cycle, expansion factors, regression analysis, ratio estimators.

ONE OF THE ENVIRONMENTAL ISSUES OF GLOBAL CONCERN TODAY is the increase in carbon dioxide in the atmosphere and its potential effect on climate. Fossil fuel combustion and cement production are two major sources of atmospheric carbon dioxide. Researchers using global terrestrial

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carbon models argue that deforestation and other land-use changes in the tropics are also a significant source of atmospheric carbon dioxide (Detwiler and Hall 1988, Detwiler et al. 1985, Houghton et al. 1985). The magnitude of this additional source is currently estimated to be between 8% and 47% of that produced from fossil fuel combustion and cement manufacture. However, these estimates ignore the potential role of mature and secondary tropical forests as sinks of atmospheric carbon dioxide (Lugo and Brown, 1986).

Estimates of the carbon dioxide flux from changes in land-use in the tropics are derived from models that keep an account of the rates of carbon release and uptake. Release of carbon is associated with land clearing for agriculture (both permanent and shifting cultivation), commercial logging, and increased oxidation of soils. Uptake of carbon is associated with reforestation and recovering forest vegetation and soils after abandonment. The uncertainty in the results from these models arises from the use and interpretation of the input data by the different groups of researchers. Two major sources of uncertainty are (1) the biomass (or carbon content) of tropical forests and (2) the rates of land use changes. This paper focuses on methods to reduce uncertainty in tropical forest biomass estimates.

Brown and Lugo (1982, 1984) have made two estimates of the total biomass (above + below ground) of tropical forests from two distinctly different data bases. For the first estimate (1982), they synthesized data from the literature on total biomass of tropical forest vegetation estimated by direct measurements on experimental plots (either by destructive harvest techniques or by applying regression equations derived from destructively harvested trees). They obtained a weighted average total aboveground biomass (TAGB)[1] for closed forests of 282 Mg/ha (a range of 144–513 Mg/ha) and for open forests of 55 Mg/ha (a range of 28–82 Mg/ha).

In the second analysis, Brown and Lugo (1984) used data reported by country for all major forest types as given by the Food and Agriculture Organization of the United Nations (1981). They converted commercial wood volumes to TAGB using average wood densities and expansion factors (ratios of TAGB to commercial biomass) and obtained a weighted average TAGB of 150 Mg/ha for undisturbed tropical closed forests and 50 Mg/ha for open forests. They two methods thus gave markedly different biomass estimates for closed forests, but similar estimates for the open forest. As most land use changes are occurring in closed tropical forests, where biomass varies the most, it is necessary to obtain more accurate and precise biomass estimates for these forests in order to improve understanding of the role of tropical forests in the global carbon cycle.

Improving the estimate of tropical forest biomass requires a broader data base than that provided by ecological studies that measure biomass directly. The few studies that measured biomass directly cover a small area of tropical forests (combined area of all studies <30 ha), and are generally biased (for our purposes) toward larger biomass plots (Brown and Lugo 1984). We believe that biomass estimation based on forest volume inventories provides an opportunity to improve the total aboveground biomass estimates because volume data from forest inventories are more abundant and are generally collected from large sample areas using a planned sampling method designed to represent the population of interest. This approach has been used in

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[1] Brown and Lugo (1982, 1984) computed TAGB, then multiplied by 1.16 to report total (above and below ground) biomass. We have used their original estimate of TAGB for consistency within this paper, which deals only with aboveground biomass.

temperate countries (e.g., Johnson and Sharpe 1983) and should be readily applicable to tropical forests as well.

Several kinds of data on tropical forests are collected during forest inventories that may be useful for estimating tropical forest biomass. For example, inventories often report stand (number of stems/ha by diameter classes) and/or stock (volume/ha by diameter classes) tables down to some minimum diameter, stratified into forest types. These tables are often based on hundreds of plots representing thousands of hectares of forest land. Forest inventories are unfortunately not standard in the types of information recorded and reported; hence we are currently developing a variety of approaches for estimating tropical forest biomass based on a variety of information sources.

The objectives of this paper are (1) to present a methodology by which various kinds of common inventory data can be used to estimate the biomass of tropical forests; (2) to demonstrate applications of these methods to tropical forests in four countries; and (3) to use the new analyses to reduce the discrepancy between the volume-based (Brown and Lugo 1984) and direct-measurement-based (Brown and Lugo 1982) estimates of closed forest biomass.

APPROACH

The paper is organized into the following sections, outlining our strategy for data analysis:

1. Develop and test a set of regression equations to estimate total aboveground biomass ($TAGB$, kg) of individual trees as a function of life zone group, diameter at breast height (D, cm), total height (H, m), and wood density or specific gravity (S, mg/m^3), and to estimate H as a function of D and life zone for use in double sampling estimates of biomass.
2. Apply these regressions to some 5300 trees from 43 independent sample plots to yield estimates of $TAGB$ per unit area by forest type. We then estimate expansion factors, defined as the ratio of $TAGB$ to commercial (stem) biomass. Commercial biomass is calculated as the product of commercial volume (as reported by the data sources) and species wood density.
3. Apply the regression equations to independent stand tables from large-scale forest inventories in four countries, yielding additional $TAGB$ estimates. Stock tables from the same inventories were combined with wood density data to obtain commercial biomass, allowing additional estimates of expansion factors.
4. Reconcile the biomass estimates reported by Brown and Lugo (1982, 1984).

The various estimates of TAGB/ha and expansion factors are compared within and across life zones to derive a generalized approach for TAGB estimation making most efficient use of whatever information is available. A critical part of this comparison (where possible) is proper estimation of errors for the various estimates, leading to confidence interval estimation. Confidence intervals are important to modelers for conducting sensitivity analyses and putting estimates of error on their model outputs. Current practice (e.g., Houghton et al. 1985, Detwiler and Hall 1988) is to use biomass estimates from a variety of sources in conducting sensitivity analyses. We hope to provide a methodology whereby a single estimate may be generated and tested with confidence intervals.

DEVELOPMENT OF BIOMASS REGRESSION EQUATIONS

We derived biomass regression equations from nine data sets (Table 1). We evaluated several linear and transformed nonlinear equations for each of

TABLE 1. *Sources, sample size (n), and range of diameter at breast height (dbh) of trees used for developing biomass regression equations.*

Life zone	Source	n	Range of dbh (cm)
Dry	Bandhu 1970	23	10–39
	Mann and Saxena 1982	5	5–40
	Vyas et al. 1972	4	10–22
Moist	Hozumi et al. 1969	72	10–130
	Jordan and Uhl[a]	42	5–65
	Russell 1983	15	10–38
	Yamakura et al. 1986	39	10–130
Wet	Edwards and Grubb 1977	41	10–110
	Ovington and Olson 1970	28	5–45

[a] C. Jordan and C. Uhl, 1986, University of Georgia, provided unpublished tree biomass data.

three forest types (wet and rain, moist, and dry forest life zones, *sensu* Holdridge 1967) with D, H, and S as predictor variables. Since forest inventories are not consistent in terms of the variables measured, we assumed that (1) D would always be measured, (2) H would sometimes be measured, and (3) S would occasionally be available if species were recorded (often not an easy task in the tropics, where identification may require a very experienced botanist or local person, and S may be known only for a few species). We therefore developed biomass equations based on D alone, equations based on D and H, and equations based on D, H, and S. At this time, we lack data to develop regressions which consider S in the wet life zone and which consider H and S in the dry life zone. Wharton and Cunia (1987) give overviews of many of the statistical methods used in developing these equations.

The initial analysis was done both by sample and by life zone. Biomass was plotted against D, H, S, and D^2H to study the range and shape of the regression relationship, and to get a rough estimate of the heterogeneity of the conditional variance. Figure 1 shows scatterplots of $TAGB$ vs. D by life zone groupings for small diameter ($D < 30$ cm, Figure 1A) and large diameter ($D \geq 30$ cm, Figure 1B) trees. Most sample trees are less than 50 cm in diameter; only 5 trees were >75 cm in diameter, with the largest sample trees around 130 cm in diameter.

The conditional variance of tree biomass increases with tree size. The variance of the biomass was computed by various classes of tree sizes and plotted, and it was decided that the conditional variance was roughly proportional to D^4 and to D^4H^2. A second set of analyses focused on the natural logarithms of the predictor variables. The logarithmic transformation has the potential to correct for the heterogeneous conditional variance of biomass.

Many researchers construct biomass regressions with nonlinear models of the form $\hat{Y} = \beta_1 X^{\beta_2}$. Taking the natural log of each side of the equation yields

$$\ln(Y) = \ln(\beta_1) + \beta_2(\ln(X)) = \alpha_1 + \alpha_2(\ln(X)) \tag{1}$$

which may be fit by the method of ordinary least squares (OLS). Several authors (e.g., Baskerville 1970, Beauchamp and Olson 1973) have warned that such transformed nonlinear models cannot simply be retransformed to the nonlinear form because this yields underestimates of up to 20% for certain components (Baskerville 1970). The bias has a simple approximate correction when the mean squared error (MSE) is not too large (Baskerville 1970):
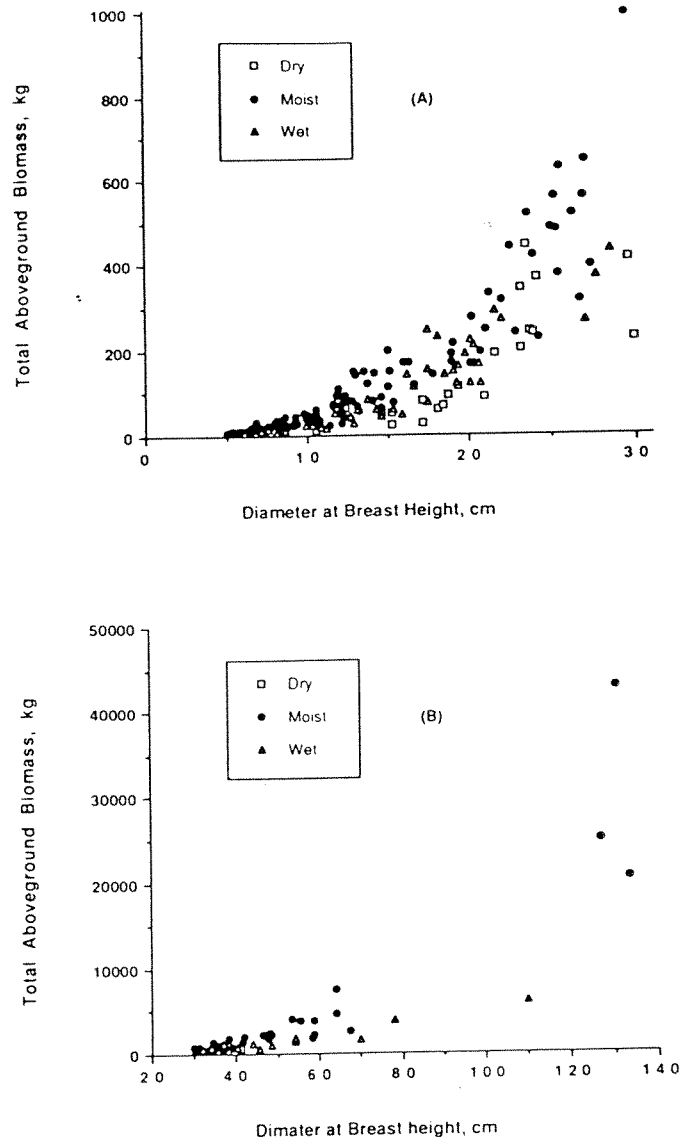
FIGURE 1. Scatterplots of total aboveground tree biomass (*TAGB*, kg) vs. diameter at breast height (dbh, cm) for the data sets available from dry, moist, and wet life zones. (A): All trees < 30 cm dbh; (B): All trees ≥ 30 cm dbh.

$$\hat{Y} = \exp(\alpha_1 + \alpha_2(\ln(X)) + MSE/2) \tag{2}$$

where "exp" denotes "e to the power of." We used this approach for those cases where the *MSE* was not too large (as determined by whether the correction improves or worsens the model fit).

The utility of the logarithmic transformation is its ability to account for the heterogeneous conditional variance of *Y* given *X*. Weighted linear models can achieve similar results, with the added benefits of inherent unbiasedness and easily expressed estimates of error. The method of weighted least squares (Cunia 1964) consists of finding some function *f(x)* which is propor-

tional to the conditional variance of Y, then dividing each observation Y and corresponding predictor variable X by the square root of $f(x)$ to create new transformed variables. Application of the OLS methods to the transformed variables yields weighted least squares estimates of the regression parameters. Based on the initial analysis, $f(x)$ for our data was assumed to be D^4 or D^4H^2 for models using D alone or D and H respectively.

We considered the following six models:

linear (weighted):

$$\hat{Y} = \beta_1 + \beta_2 D + \beta_3 D^2$$

$$\hat{Y} = \beta_1 + \beta_2 (D^2H)$$

$$\hat{Y} = \beta_1 + \beta_2 (D^2HS)$$

transformed nonlinear:

$$\widehat{\ln Y} = \beta_1 + \beta_2 \ln D$$

$$\widehat{\ln Y} = \beta_1 + \beta_2 \ln(D^2H)$$

$$\widehat{\ln Y} = \beta_1 + \beta_2 \ln(D^2HS)$$

We tested for differences between the individual samples within each life zone using analysis of covariance. The final regressions were also tested across life zones to consider whether separate equations by life zone were needed. Studentized ordinary and PRESS residuals were compared and plotted to check for outliers, influence, and model fit. Residual analysis indicated that the few large trees did not in general exert undue influence upon the estimated regression equation. We computed an adjusted R^2, also known as a "fitness index" (Schlaegel 1985), using the residuals between the original values of Y and the retransformed estimates of Y. The adjusted R^2 measures the amount of sample variation (in original units) which is accounted for by the regression equation relative to the total sample variation. We plotted each equation well beyond the range of our data, to examine how reasonable the model seemed upon extrapolation. We selected our final models (Table 2) based on the residual and graphical analysis and the adjusted R^2. As there were relatively few large trees in our samples, we chose

TABLE 2. *Regression equations for estimated total aboveground biomass (Y kg/ tree) and total height (H, m) in tropical forests by life zone group.*[a]

	Life zone	Equation[b]	n	R^2 (adj)	MSE
[1]	Dry	$\hat{Y} = 34.4703 - 8.0671\ (D) + 0.6589\ (D^2)$	32	0.67	0.02208
[2]	Moist	$\hat{Y} = 38.4908 - 11.7883\ (D) + 1.1926\ D^2$	168	0.78	0.06181
[3]		$\hat{Y} = \exp\{-3.1141 + 0.9719\ \ln\ (D^2H)\}$	168	0.97	0.1161
[4]		$\hat{Y} = \exp\{-2.4090 + 0.9522\ \ln\ (D^2HS)\}$	94	0.99	0.06079
[5]		$\hat{H} = \exp\{1.0710 + 0.5677\ \ln\ D\}$	3824	0.61	0.07495
[6]	Wet	$\hat{Y} = 13.2579 - 4.8945\ (D) + 0.6713\ (D^2)$	69	0.90	0.02247
[7]		$\hat{Y} = \exp\{-3.3012 + 0.9439\ \ln\ (D^2H)\}$	69	0.90	0.2110
[8]		$\hat{H} = \exp\{1.2017 + 0.5627\ \ln\ D\}$	69	0.74	0.4299

[a] The transformed nonlinear models include the adjustment term (MSE/2) along with the intercept, when appropriate.

[b] "Exp" denotes "e to the power of . . .", D = dbh in cm, H = total height in m, and S = wood density in Mg/m^3 = g/cm^3.

models which were expected to behave reasonably upon extrapolation up to 300 cm D, our assumed maximum stand diameter for tropical forests. We acknowledge that extrapolation beyond the range of actual observations is not statistically valid. However, at this time we lack alternative means of assigning biomass to the largest trees, hence we chose models which seemed to project reasonably, based on our experience in the tropics. Note that in most cases we apply the biomass regressions to stand tables where diameter classes are well within the domain of our data, so area-wide estimates of biomass should remain reasonable. In the one case where we have individual tree data (Venezuela), only 15 out of 5307 trees are beyond the range of our data. These trees are estimated to account for less than 10% of the total stand biomass.

Analysis of covariance implied that the samples within the dry life zone could be grouped, as could the samples within the wet life zone. Within the moist life zone, the analysis indicated that the regressions from the four samples were not homogeneous except when the regression model considered D, H, and S. This implies that there are differences among some of the samples (probably relating to different species mixes with different wood densities), and that a better fit is obtained when one considers sample membership. However, this life zone may be considered to be a population of interest, with the independent samples being considered to be a subsample from this population. For practical purposes, it is desirable to obtain an estimate of the regression relationship for this population; thus, the combined regressions for pooled data sets in each life zone grouping are reported in Table 2. We recognize the variability inherent in this population, and that more samples are needed to construct a proper regression for the entire life zone, particularly in the larger tree size classes (cf Figure 1b). However, we feel that the equations reported in Table 2 are the most appropriate for the global focus of terrestrial carbon models. This grouping within life zones is consistent with an earlier report by Crow (1978), who found no important differences between $TAGB$ regressions from tropical forests in two different countries. Analysis of covariance indicated that the samples could not be grouped across life zones without a statistically significant loss of information.

A comparison across life zones of regressions based on diameter alone illustrates that a tree of given diameter has more biomass in the moist life zone than in the wet or dry life zones, because trees in the moist life zone tend to be taller than trees in wet and dry life zones. This agrees with Brown and Lugo (1982) who reported that standing biomass as well as productivity was maximized in moist life zones, and declined as moisture increased or decreased. Given data from more life zones, it might be possible to construct a response surface of biomass as a function of tree attributes (diameter, height, and density) and environmental attributes (potential evapotranspiration or temperature/precipitation ratio). Our three regressions for dry, moist, and wet forest represent discrete "slices" through such a continuous response surface.

DOUBLE SAMPLING ESTIMATORS

A biomass equation considering both D and H should yield better estimates than an equation using D alone, because of the additional information imparted by knowledge of H. However, most large scale forest inventories do not measure H due to time and cost constraints. One way to improve biomass estimates is to use auxiliary information derived from other popula-

tions and presumed to apply to the population in question. The potential benefit is increased precision and accuracy because of the increased amount of information (Cunia, 1986). This is true when the auxiliary information fits the population under consideration. When the populations are different, and the auxiliary information does not fit, then the potential cost is loss of accuracy (increased bias).

Double sampling estimates, where a relationship derived from one sample is applied to another sample, is one such method of incorporating auxiliary information. We have developed regression equations by life zone to estimate H as a function of D for trees where H is not known. The estimate of H and the measured D are then used to estimate biomass, using one of the equations in Table 2. Michelakackis and Cunia (1987) describe double sampling for biomass estimation.

The H-D relationships are based on about 4000 measured trees from 35 wet and moist sites in Venezuela, Puerto Rico, and Papua-New Guinea. We did not develop a H-D relation for the dry life zone group because there is no biomass equation which uses H as a predictor variable. We tested linear, hyperbolic, and transformed nonlinear models, and chose the transformed nonlinear model based on residual analyses, adjusted R^2, and graphical analysis. In general, hyperbolic models underestimate H for large trees, while linear models overestimate H upon extrapolation. We estimated H with a transformed nonlinear model [estimates adjusted with Baskerville's (1970) correction]:

$$\widehat{\ln H} = \beta_1 + \beta_2 \ln D \tag{3}$$

Analysis of covariance indicated a better model fit when regression considered plot membership, which is reasonable since H-D relationships are known to vary geographically with site quality (Baker 1950). However, as plot membership presumably reflects variable environmental site conditions, we chose to ignore differences between plots in an attempt to estimate an average H-D relationship for each life zone. The final equations are included in Table 2.

APPLICATION OF BIOMASS REGRESSION EQUATIONS TO PLOT DATA

Methods

We applied the equations of Table 2 to individual trees from 32 moist, 9 moist-transition-to-dry, and 2 dry life zone plots to estimate $TAGB$/ha. We applied the regressions for the moist forest to the plot data from moist-transition-to-dry forest because, although dryer, this forest type maintains more characteristics in common with the moist forest than with the dry forest (Holdridge 1967). Detailed plot data as required for this analysis are not generally available to researchers outside the country of interest, hence our geographic coverage is at this time restricted to Venezuela and Brazil as examples of methodology (Table 3). Most of the data came from the personal records of J. P. Veillon, Universidad de Los Andes, Merida, Venezuela. The minimum tree diameter included in sample plots ranged from 5 to 25 cm (Table 3). Because of the relatively large minimum diameter of Heinsdijk's Brazilian plots (1985a,b), our estimates of $TAGB$ per unit area for these plots are probably low. In another study in similar forest (Heinsdijk 1957), stems from 5 to 24 cm were included and by our methods represent approximately 15% of the stand biomass.

TABLE 3. *Description of plot data base used in estimating total aboveground biomass and expansion factors, arranged by life zone groups. dbh = diameter at breast height.*

Country and life zone	Elevation (m)	Number of plots	Size of plots (ha)	Minimum dbh (cm)	Volume determination	% stems of known S^a	Source
T-Moist Forest							
Brazil	Lowlands	2	1	25	Given in source	85	Heinsdijk 1958a,b
Brazil	Lowlands	2	0.08	5	Calculated from equation given in source[b]	29	Prance et al. 1976
Venezuela	35–1100	17	0.06–0.25	10	From published volume tables[c]	74	Veillon 1985, Veillon 1986, pers. comm.
	1500–2500	11	0.25	10	From published volume tables[c]	64	Veillon 1985, Veillon 1986, pers. comm.
T-Moist Transition Dry Forest, Venezuela	100–220	9	0.25	10	From published volume tables[c]	85	Veillon 1985, Veillon 1986, pers. comm.
T-Dry Forest, Venezuela	170	2	0.25	10	From published volume tables[d]	81	Veillon 1985, Veillon 1986, pers. comm.

[a] S = wood density.
[b] Volume = basal area × stem height × 0.70 (recalculated by us)
[c] Veillon and Silva 1972.
[d] Veillon 1970.

We used standard regression techniques to estimate $TAGB$. Let $[b]$ = the m by 1 vector of estimated regression coefficients from some model, $[S_{bb}]$ = the m by m estimated covariance matrix of $[b]$, and let $[\mu]$ = the m by 1 vector of means per ha for the m predictor variables included in the model. The mean and variance of $Y = TAGB/$ha are estimated by $Y = [b]'[\mu]$ and $S_{yy} = [\mu]'[S_{bb}][\mu]$ respectively. Table 4 lists the point and 95% confidence interval estimates of $TAGB/$ha resulting from the application of the biomass regressions to the plot data. The estimate of $TAGB$ and its variability consistently decreased as regressions included more predictor variables. The decrease was not significant for the moist life zone, but there was a significant difference in the moist-dry transition zone between regressions based on D alone and regressions which included actual H.

We determined commercial biomass to estimate ratios of $TAGB$ to commercial biomass, herein called *expansion factors*. Commercial volumes for individual trees were either given by the sources of data or were obtained from published volume tables (Table 3). Commercial biomass per plot was determined as the summation of the products of commercial volume and wood density over all trees in the sample plot. Several hundred different species were represented in our data sets. Although wood density was not known for all species, it was generally available for 65%–85% of the stems on a given plot (Table 3). For species with unknown wood density, we

TABLE 4. *Estimates of total aboveground biomass and expansion factors (mean and 95% confidence interval) resulting from the application of biomass regression equations to sample plots in tropical moist, moist transition to dry, and dry forest life zones of Tropical America.*

	Life zone[a]		
	Moist	Moist Δ Dry	Dry
Number of plots:	32	9	2
Stem volume (m³/ha):	330.06	189.99	119.27
Stem biomass (Mg/ha):	194.83	108.14	70.11
Total aboveground biomass (Mg/ha)[b] based on:			
D	374.52	276.05	110.14
95% CI	(347.06–401.99)	(255.35–296.75)	(91.04–129.24)
D and $\hat{H}$[c]	363.35	264.66	—
95% CI	(341.90–386.14)	(248.18–282.23)	
D and H	344.56	220.54	—
95% CI	(320.41–370.53)	(204.89–237.38)	
D, H, and S	339.59	211.16	—
95% CI	(320.59–359.72)	(199.26–223.76)	
Expansion factor (±95% CI)[d]:			
D	1.922 ± 0.156	2.553 ± 0.497	1.571
D and $\hat{H}$	1.865 ± 0.194	2.447 ± 0.610	—
D and H	1.768 ± 0.136	2.039 ± 0.340	—
D, H, and S	1.743 ± 0.083	1.953 ± 0.074	—

[a] All life zones are tropical; Δ = transition.

[b] Calculated from appropriate regression equations in Table 2, where D = diameter at breast height, H = total height, S = wood density, and $\hat{H}$ = estimated height. The 95% confidence intervals are not symmetric for nonlinear regressions. The equations for moist forest were used in the moist transition to dry life zone.

[c] Double sampling confidence intervals include errors from both regressions.

[d] Expansion factor = total aboveground biomass/stem biomass, ±95% confidence interval where possible to compute (see text for further explanation).

substituted the arithmetic mean of the known species on the same plot. Species of unknown wood density were generally minor components of the plots in terms of volume and biomass. Wood densities for species ranged from 0.20 to 1.05 g/cm^3 and are on file by species at the Institute of Tropical Forestry, Río Piedras, Puerto Rico. Average commercial volume (m^3/ha) and commercial biomass (Mg/ha) by life zone groups are reported in Table 4. It was not possible to include confidence intervals with these estimates, as the error of the volume estimation is unknown.

RESULTS

The moist life zone has the most biomass per unit area, followed by moist-dry and dry life zones. This is consistent with earlier work of Brown and Lugo (1982); trees in the moist life zone presumably have the most favorable water balance, which optimizes biomass accumulation relative to other life zones.

The biomass expansion factors were determined using the ratio-of-means estimator given by Cochran (1977). There were enough moist and moist-dry transition plots (n $\geq$ 5) to permit estimation of the sample variance, so that 95% confidence intervals are included with the ratios. Ratios were computed using biomass estimates based on all biomass regressions available for each life zone group. Our best estimates imply expansion factors of 1.74, 1.95, and 1.57 for undisturbed primary forests in moist, moist-dry, and dry life zones respectively (Table 4). There is no discernible difference between the expansion factors estimated for moist and moist-dry transition life zones except when S is included in the estimation of $TAGB$.

Our new expansion factors can be compared to the earlier expansion factor estimates[2] of Brown and Lugo (1984) of 1.1 to 1.6 across all life zones. Therefore these new ratios represent an increase in estimated ratios of $TAGB$ to commercial biomass. These new estimates are also comparable to estimates of 1.25 to 1.82 for temperate forests (Johnson and Sharpe 1983) estimated by an approach similar to ours.

APPLICATION OF REGRESSION EQUATIONS TO STAND AND STOCK TABLES

METHODS

There are many forest inventories for tropical countries. For this paper, we limited consideration to those inventories readily available to us which met the following criteria: the minimum tree diameter measured was ≤ 15 cm, all species were counted, and commercial volumes were presented by species or species groups. We also chose inventories representing four different tropical forested regions (America, Africa, south Asia, and southeast Asia), and are currently in the process of completing a forest inventory database for south and southeast Asia as part of the Tropical Land Use/CO_2 project sponsored by the U.S. Department of Energy through Oak Ridge National Laboratory.

We estimated $TAGB$ from stand tables by applying a biomass regression equation from Table 2 to the midpoint of the diameter classes to estimate the biomass per tree. $TAGB$ of all trees in a given diameter class was obtained

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[2] Published values were the ratio of total (above and below ground) biomass to commercial biomass. The range reported here is based on recalculation without belowground biomass.

by multiplying the biomass per tree by the number of stems/ha in the diameter class. This was repeated for all diameter classes, and the biomass estimates per class summed to give the *TAGB*/ha. We report in most cases two estimates of *TAGB* from each stand table: one estimate using a regression based on *D* alone, and a second estimate using the double sampling approach. Double sampling was not applied to stands in the dry life zone, due to lack of appropriate equations.

Calculation of commercial biomass required estimates of commercial volume and wood density. We consulted many sources and found wood densities for about 50% of the species and in some cases for as many as 70% (Table 5). For those species or species groups for which no wood density data were available, an arithmetic mean of those that we had for a given forest type was computed and substituted for the missing values. Total commercial biomass/ha was computed as the sum of the products of commercial volume and wood density for each species or species group. Expansion factors were computed as the ratio of *TAGD*/ha and commercial biomass/ha. Mean expansion factors by forest type and 95% confidence intervals were computed from the ratio of the mean TAGB and stem biomass as described in the previous section. In all cases *TAGB* computed using *D* alone was higher than *TAGB* based on *D* and *H* (Table 6). This is similar to results reported earlier, and suggests that the regression based on *D* alone might tend to slightly overestimate *TAGB* when applied to a stand table (assuming that our method of height estimation is accurate). We believe that the double sampling estimates of *TAGB* are more accurate than those based on *D* alone, as we feel the *H-D* relationships are realistic.

RESULTS

Total aboveground biomass varies by geographical region, life zone, forest type, forest structure, and degree of disturbance. Primary moist forest *TAGB* in the four countries is highest in Malaysia (a range of 255–446 Mg/ha across 15 inventory subunits in moderate, good, and superior hill forests), followed by Cameroon (238–314 Mg/ha across 20 inventory subunits), French Guiana (280 and 283 Mg/ha for two inventory subunits), and Sri Lanka (153–221 Mg/ha across 14 inventory subunits). Primary moist forest biomass in Cameroon, French Guiana, and Malaysia is within the range of those for other forest types within this life zone (245–513 Mg/ha, based on direct measurements) reported by Brown and Lugo (1982). Biomass for the Sri Lankan moist forests is considerably lower than the other forest areas, which may suggest that these forests are more disturbed than reported by the authors of the inventory. Forest biomass decreased with increasing intensity of disturbance in Malaysia and Sri Lanka, but increased with disturbance in French Guiana. This apparent increase in French Guiana may be due to different initial site qualities and biomass carrying capacities.

The expansion factors vary greatly between as well as within countries and life zones (Table 6). Expansion factors based on *D* alone are consistently greater than expansion factors obtained via double sampling, reflecting the higher estimates of *TAGB* based on *D* alone (as the denominator of the expansion factor is constant). We hypothesize that the differences in expansion factors between and within the different countries is due to differences between the average tree sizes in the inventoried forests. The ratio of *TAGB* to commercial tree biomass is clearly dependent upon many things, including tree size and definition of "commercial biomass." All trees have some positive *TAGB;* however, trees below a certain arbitrary commercial size are

TABLE 5. *Description of forest inventories from which expansion factors are estimated.*

Country	Life zone	# of plots inventoried	Plot size (ha)	# forest categories	Minimum dbh (cm)	Volume determination[a]	# of species	% known S[b]	Source
Cameroon	T-moist	400	0.5	1	15	Local volume tables for 34 major species or species groups	401	70	Centre Technique Forestiere Tropical 1969
French Guiana	T-moist	951	0.5	3	10	Local volume tables by species groups	240	70	Centre Technique Forestiere Tropical 1975
Peninsular Malaysia	T-moist	4608	0.1	11	15	Local volume tables by species group	38 species groups, 1-54 species/group	≈50	United Nations Development Program 1972
Sri Lanka	T-moist, t-dry, and dry transition to moist	6899	Variable, based on a 10-factor prism	18	10	Basal area × stem height × form factor (0.7 for moist and 0.65 for dry)	161 moist, 86 dry	47 moist, 47 dry	Andrews 1961; McCormick 1961; McCormick & Pillai 1961a, 1961b, 1961c, 1961d, 1961e; Nisbet 1961a, 1961b, 1961c, 1961d

a Commercial volume from stump point to crown point. Volume is reported as overbark for all countries except Malaysia which reports underbark.
b Percent of the recorded species for which we were able to obtain wood density data.

TABLE 6. Stand characteristics, volume, and estimates of aboveground biomass and expansion factors based on forest inventory data for forests in three geographically different tropical regions (refer to table 5 for descriptions of inventories).

Forest Type	Number of Inventory Subunits	Tree density (# stems/ha)	Basal area (m²/ha)	Stem volume (m³/ha)	Stem biomass (Mg/ha)	TAGB[a] (D) (Mg/ha)	Expansion factor (1)[b] (±95% CI)	TAGB[a] (D & H) (Mg/ha)	Expansion factor (2)[b] (±95% CI)
Cameroon Tropical Moist Forest									
Primary	20	221.7	26.4	307.7	199.2	312.1	1.567 ± 0.051	279.2	1.402 ± 0.038
Sri Lanka Tropical Moist Forest									
Primary forest	8	384	19.5	152.1	87.6	205.3	2.343 ± 0.327	177.3	2.024 ± 0.262
Medium yield	3	450	21.7	169.7	95.6	216.8	2.267	185.5	1.940
Low yield	3	400	16.0	98.9	54.3	159.1	2.929	132.7	2.444
Nonproductive	3	651	12.9	42.3	22.2	119.8	5.387	99.4	4.477
Secondary	3	386	15.1	100.3	55.4	149.8	2.702	124.9	2.255
Young secondary	3	192	4.4	19.1	10.6	43.7	4.132	36.2	3.415
Sri Lanka Dry to Moist Transition Forest[c]									
Medium yield	1	307	17.6	81.4	51.7	93.7	1.812	—	—
Low yield	1	339	15.9	55.7	36.4	83.4	2.291	—	—
Nonproductive	1	317	10.8	40.4	25.8	51.7	2.004	—	—
Sri Lanka Tropical Dry Forest									
Medium yield	6	433	21.1	78.9	52.0	117.1	2.253 ± 0.204	—	—
Low yield	8	417	16.6	52.1	34.2	85.5	2.505 ± 0.260	—	—
Nonproductive	2	336	9.9	24.1	15.7	47.4	3.019	—	—

Malaysia Tropical Moist Forest								
Superior Hill Forest	5	289	32.4	362.0	202.9	391.0	1.927 ± 0.055	382.1	1.833 ± 0.107
Good Hill Forest	5	250	28.5	313.5	176.5	344.0	1.949 ± 0.143	334.4	1.895 ± 0.185
Moderate Hill Forest	5	250	25.0	280.9	159.1	296.3	1.863 ± 0.141	278.9	1.753 ± 0.173
Logged Hill Forest	5	220	22.0	249.2	141.3	260.9	1.846 ± 0.105	245.4	1.737 ± 0.114
Disturbed Hill Forest 1	6	176	15.0	165.9	93.2	172.3	1.848 ± 0.127	156.3	1.677 ± 0.161
Disturbed Hill Forest 2	1	177	18.4	193.7	110.4	219.6	1.989	210.0	1.902
Poor Hill Forest	1	179	15.4	169.1	95.3	176.9	1.856	159.6	1.675
Upper Hill Forest	1	250	22.0	236.5	135.2	254.9	1.885	231.7	1.714
Freshwater Swamp Forest	1	273	17.4	204.1	111.7	188.7	1.689	161.7	1.448
Logged Freshwater Swamp Forest (since 1966)	1	116	10.9	112.8	62.6	126.6	2.022	113.7	1.816
Disturbed Freshwater Swamp Forest (prior to 1966)	1	134	9.9	101.8	57.1	111.1	1.946	99.2	1.737
French Guiana Tropical Moist Forest								
Closed Forest-Primary	2	313	26.5	302.3	210.4	314.1	1.493	280.3	1.332
Closed Forest-Disturbed	3	507	27.6	305.5	206.8	319.7	1.546	277.6	1.342
Open Forest/Savanna Forest	2	304	13.2	144.4	102.0	148.6	1.458	126.5	1.24

[a] $TAGB$ = total aboveground biomass based on regression equations in Table 2, D = dbh and H = height as the independent variables.
[b] Expansion factor (1) = $TAGB$ using D only/stem biomass and expansion factor (2) = $TAGB$ using D and H/stem biomass. Mean expansion factors were calculated as the ratio of the mean total biomass and mean stem biomass. CI = confidence interval (see text for further discussion). Confidence intervals only given when $n \geq 5$ inventory subunits were available.
[c] This life zone has more in common with the dry life zone, hence the dry biomass equations are applied.

said to have no commercial biomass. As *TAGB* is always greater than commercial biomass, the ratio approaches infinity as commercial biomass approaches zero, i.e., for smaller trees. The ratio is undefined for trees with no commercial biomass, as division by zero is undefined. As trees get larger, proportionately more of the biomass is commercial, hence the ratio will decrease. When a tree reaches maximum height, further growth takes place as diameter and crown increment and the ratio may well approach some constant.

The quadratic stand diameter (*QSD*) is a useful index for describing the average size of trees in a stand. It is readily available from many inventories which report basal area and numbers of stems per unit area. The *QSD* is the quadratic mean of the diameter of trees in a stand, or the diameter of a tree of average basal area (*BA*):

$$QSD = \sqrt{\{(\Sigma D^2)/n\}} = \sqrt{\{(BA/n) * (4/\pi)\}} \tag{4}$$

Figure 2 shows that the expansion factor of a forest is related to the size of trees comprising the forest. Once differences in expansion factors between stands are removed by consideration of *QSD*, then differences between regions and life zones mostly disappear. The sampled forests in Sri Lanka have high expansion factors because they have proportionally smaller trees. The sampled forests in Cameroon have lower expansion factors because they have larger trees. The Malaysian forests are between Sri Lanka and Cameroon in terms of *QSD* and expansion factors. The French Guianan forests have lower expansion factors than expected, which may be related to the method of volume determination. The expansion factor starts very high
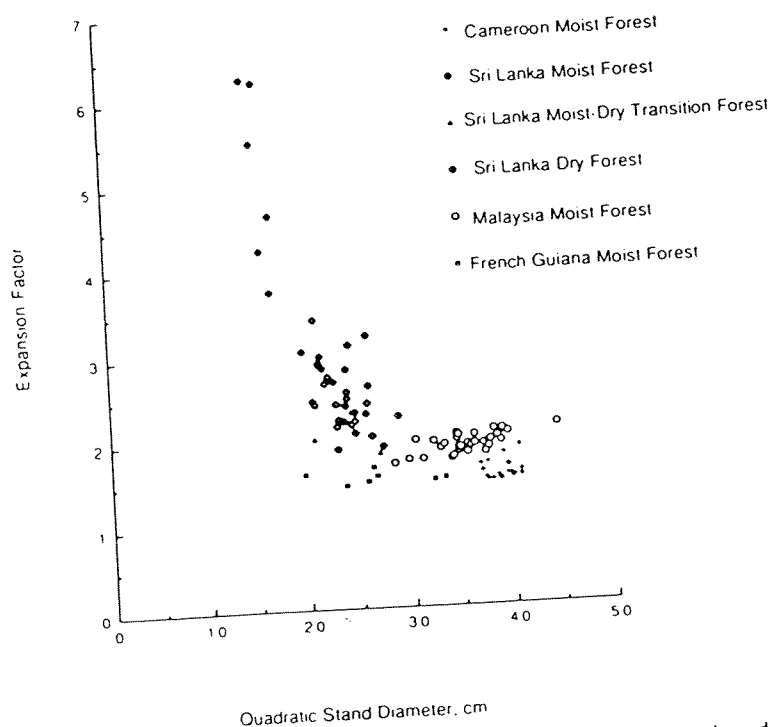

FIGURE 2. The relationship between expansion factors (biomass) based on diameter at breast height and quadratic stand diameter (*QSD*, cm)

for forests with a low *QSD*, and seems to approach an asymptote of 1.50–2.00 for forests with $QSD \geq$ about 30 cm.

There seems to be no single expansion factor appropriate for all forests within a given life zone or geographic region. Rather, the expansion factor seems heavily dependent upon the relative sizes of trees comprising a stand. Therefore one should not unknowingly apply expansion factors to forests without some knowledge of average tree size, or at least of stand conditions which may permit assumptions regarding average tree size. In contrast, expansion factors seem relatively insensitive to life zone when *QSD* is constant.

This has important implications for biomass estimation. Undisturbed mature primary forests with $QSD \geq 30$ cm in all life zones probably have expansion factors around 1.50 to 2.00. The ratio will vary for disturbed forests, depending on the method and reason for disturbance. For example, a forest which has been selectively logged will probably have a lower QSD than before, so the expansion factor will increase. A recovering secondary forest or plantation may initially have a high expansion factor which then decreases over time, as the trees get larger. Clearly further work is needed to study the relationship between expansion factor and tree size, to see how this relationship behaves over a wider range of forest types. We fit a piecewise regression through the points on Figure 2 to tentatively estimate biomass expansion factors for tropical forests as a function of *QSD*:

$$\text{Expansion Factor} = \begin{cases} \exp(5.7671 - 1.5309*(\ln(QSD)), & \text{for } QSD < 30 \text{ cm} \\ 1.75 & \text{for } QSD \geq 30 \text{ cm} \end{cases}$$

(5)

(Adjusted $R^2 = 0.77$, $MSE = 0.03103$, $n = 82$; intercept is corrected for bias)

Equation (5) uses expansion factors based on *TAGB* estimates using *D* alone. A similar equation using expansion factors based on the double sampling estimates yielded estimates approximately 8% lower. Equation (5) applies to inventories similar to those described in Table 5. Different inventories may require different models. The minimum size class included in inventories will affect the ratio because determination of the smallest size class affects the *QSD* by including or excluding smaller trees, which may decrease or increase *QSD* accordingly. The method of volume determination also affects the ratio, as commercial biomass is determined from volume and wood density.

TOTAL ABOVEGROUND BIOMASS ESTIMATES OF TROPICAL CLOSED BROADLEAF FORESTS

Brown and Lugo (1984) estimated the biomass of tropical forests using commercial wood volume data as reported in FAO (1980) and a constant expansion factor which included above and below ground biomass. Limiting ourselves strictly to aboveground biomass, we have refined the estimates of expansion factors in this paper and have applied these new values to the FAO data base (1981) for closed broadleaf forests to yield new estimates of total aboveground biomass (Table 7). We used Figure 2 to estimate TAGB to commercial biomass expansion factors of 1.75, 1.90, and 2.0 for undisturbed, logged, and nonproductive forests respectively, these being the classifications used by the FAO in reporting areas of forest. We believe that these new expansion factors are more reliable than those used in the earlier study

TABLE 7. *Aboveground biomass estimates of closed tropical broadleaf forests based on volumes (areas, volumes, and stemwood biomass are from Brown and Lugo 1984).*

Region	Undisturbed	Logged	Nonproductive
Tropical America			
Area (10^6 ha)	452.98	53.5	147.45
Volume (10^9 m^3)	71.07	6.37	13.21
Stemwood Biomass (10^9 Mg)	43.92	3.94	8.19
Total Biomass (10^9 Mg)	76.86	7.49	16.38
Weighted biomass (Mg/ha)	169.68	139.93	111.09
Tropical Africa			
Area (10^6 ha)	118.18	43.57	52.66
Volume (10^9 m^3)	30.3	8.41	7.35
Stemwood Biomass (10^9 Mg)	17.56	4.87	4.26
Total Biomass (10^9 Mg)	30.73	9.25	8.52
Weighted Biomass (Mg/ha)	260.03	212.37	161.79
Tropical Asia			
Area (10^6 ha)	97.26	94.62	100.08
Volume (10^9 m^3)	20.97	9.7	14.45
Stemwood Biomass (10^9 Mg)	11.93	5.51	8.2
Total Biomass (10^9 Mg)	20.88	10.47	16.48
Weighted Biomass (Mg/ha)	214.66	110.64	164.67
Total tropics			
Area (10^6 ha)	668.42	191.69	300.19
Volume (10^9 m^3)	122.34	24.48	35.01
Stemwood Biomass (10^9 Mg)	73.41	14.32	20.69
Total Biomass (10^9 Mg)	128.47	27.21	41.38
Weighted Mean Biomass (Mg/ha)	192.2	141.94	137.85
Weighted Mean Biomass from Brown and Lugo, 1984 (Mg/ha)[a]	149.6	101.7	93.8

[a] Recalculated without roots (assuming a root to shoot ratio of 0.16 [Brown and Lugo 1984]).

because they are based on a broad database of commercial inventories and tree biomass measurements, and because the new expansion factors allow for the effect of forest quality or disturbance on the determination of expansion factors. Weighted (by area) *TAGB* estimates of tropical closed forests ranges from 138 to 192 Mg/ha. Undisturbed closed broadleaf forests in tropical Africa have the highest average biomass, followed by tropical Asia and America.

Although the new weighted TAGB estimates are 1.28–1.47 times higher than previously reported (Brown and Lugo 1984), even the highest value is still noticeably lower than the average of 282 Mg/ha based on direct measurement by destructive sampling (Brown and Lugo 1982). We believe that the higher direct-measurement-based biomass estimates do not accurately reflect the tropics as a whole, due to the unrepresentative sampling of measurement sites, and that the lower, volume-based estimates are thus more suited for global analyses. Results from this analysis can no longer support use of the higher, direct measurement based estimates of TAGB in global terrestrial carbon models.

CONCLUSIONS

We recommend a two-tier approach for estimating *TAGB* for tropical forests based on forest inventory data:

1. Given stand tables from forest inventories, then the regression equations may be applied to the stand tables. This method will generally be unbiased when the stems are uniformly distributed within the size classes. When the largest size class is open ended (i.e., no upper D limit is given), a common sense number should be chosen for the average D in that class. When the stand tables are derived from a well-designed forest survey, the biomass estimates may be applied to the population represented by the stand tables.

2. When the only information available is an estimate of the commercial biomass, then one may use an expansion factor based on the quadratic stand diameter and Equation (5) above. The expansion factor ranges between 1.50 and 2.00 for undisturbed primary forest, and increases up to 7.0 or more for disturbed or recovering forests. When commercial volume is available, one may use the average stand wood densities reported in this paper to convert to commercial biomass, then expand to TAGB. These estimates will generally be less precise than the methods reported above; however, in many cases, they may be the only estimates available.

We feel that the equations reported in this paper are the best available for the tropics as a whole; however, one must have caution in applying them to any specific region. Local biomass regressions based on trees from the population of interest will generally be more reliable than our equations, which are intended for a more global usage. Our equations could undoubtedly be improved by more data, particularly in the larger size classes; however, such data are currently lacking for the tropics.

Our estimates of biomass equations and expansion factors are based on data sets that consider only live trees, and do not consider litter or standing dead trees. This has been shown to lead to underestimation of $TAGB$ in temperate forests (Johnson and Sharpe 1983). However, we feel that this is less of a problem in the tropics. Tropical forests tend to carry relatively more of their biomass in the standing crop than do temperate forests, particularly when not limited by water. Therefore tropical forest inventories which ignore dead matter will nonetheless include proportionally more of the total aboveground biomass than similar inventories in the temperate zones. We currently have no data to allow estimation of the fraction of aboveground dead biomass.

There is currently increasing interest in the use of remote sensing techniques to inventory forest biomass (e.g., Sader 1988, Nelson et al. 1988). Remote sensing techniques are valuable tools which should be developed and used where possible; however, there are technical problems in the tropics that must be resolved before the full potential of remote sensing is realized. The accuracy of remote sensing depends in part on the ability to calibrate measurements with ground checks, yet many areas of tropical forest are unmapped and difficult to assess on the ground. Remote sensing techniques do not measure biomass directly; instead, they measure associated forest characteristics, e.g., crown reflectivity by satellite (Sader 1988) or tree height by laser measurements (Nelson et al. 1988). Thereafter, these techniques still rely upon some kind of equation to estimate biomass as a function of the associated variables. The approach described in this paper is similar to approaches used for decades to estimate forest volume, is familiar to most foresters, is accurate given sufficiently accurate regressions and stand tables, can readily be applied to existing data bases of current and past forest inventories and incorporated into future forest inventories, and is a prerequisite for calibration of remotely sensed information.

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