P

Forest Ecology and Management, 48 (1992) 69–87
Elsevier Science Publishers B.V., Amsterdam

Tropical forest biomass estimation from truncated stand tables

Andrew J.R. Gillespie[a], Sandra Brown[b] and Ariel E. Lugo[a]
[a]*Institute of Tropical Forestry, USDA Forest Service, Southern Forest Experiment Station, Call Box 25000, Rio Piedras, 00928-2500, Puerto Rico*
[b]*Department of Forestry, University of Illinois, 110 Mumford Hall, 1301 W. Gregory, Urbana, IL 61801, USA*

(Accepted 2 May 1990)

ABSTRACT

Gillespie, A.J.R., Brown, S. and Lugo, A.E., 1992. Tropical forest biomass estimation from truncated stand tables. *For. Ecol. Manage.*, 48: 69–87.

Total aboveground forest biomass may be estimated through a variety of techniques based on commercial inventory stand and stock tables. Stand and stock tables from tropical countries commonly omit trees below a certain commercial limit, often ≥ 35 cm. Biomass estimates made from such tables will fail to include from 25–45% of the total stand biomass. Using stand tables generated for large forested areas, we describe several methods of estimating the numbers of stems in one or two missing small-diameter classes (truncated stand tables) based on the numbers of stems in the larger size classes. We show that an exponential model reasonably approximates diameter distributions among most diameter classes in various types of tropical moist forest. The most accurate method of estimating the number of stems in smaller (missing) diameter classes used the ratio of the numbers of stems in the two smallest diameter classes. The error of estimation of total stand biomass using this approach (10–12%) was always less than the error incurred by omitting the missing classes (25–45%).

INTRODUCTION

There is increasing interest in estimating the biomass of tropical forests for both practical forestry issues and scientific purposes. Forest biomass is important for commercial uses (e.g., fuelwood assessment) and national development planning, as well as for scientific uses such as studies of ecosystem productivity, energy and nutrient flows, and for assessing the contribution of changes in tropical forest lands to the global carbon cycle. However, there is only a limited data base on biomass estimates for the tropics (Brown and Lugo, 1982; Cannell, 1982, 1984; Brown et al., 1989). Most biomass studies have been done by tropical ecologists who have different interests and research foci, vis. nutrient cycling or productivity. Their data are carefully collected, but are generally limited to small, non-randomly selected areas and are thus inadequate for the global focus of projects such as atmospheric carbon research (Brown et al., 1989).

Foresters have for decades compiled comprehensive volume inventories of many of the tropical forests in the world. Individual nations, as well as international organizations such as the United Nations Food and Agriculture Organization (FAO), have sponsored many extensive forest surveys for purposes of quantifying potentially commercial timber resources, usually reporting stand tables (number of trees per unit area by size class) and stock tables (volume per unit area by size class) by forest type and region.

Inventory data such as these can be used to make inferences about total above-ground biomass in tropical forests (Brown et al. 1989). However, the minimum diameter of sampled trees in many tropical forest inventories is often > 35 cm, reflecting the dominant interest in larger commercial timber. This is acceptable for inventories of commercial volumes, but unacceptable for biomass estimation unless adjustments are made for the missing trees.

Most of the natural forests in the tropics are uneven-aged, containing trees of all size and age classes. Although smaller trees have less volume than larger trees, the smaller size classes tend to contain relatively more trees than the larger size classes, so that in certain cases the small size classes may contain important proportions of total stand biomass (Fig. 1). The potential effect of omission of small trees was treated implicitly in earlier work (e.g. Johnson and Sharpe, 1983; Brown et al. 1989) by limiting consideration to inventories which included all stems greater than some small lower limit, say 10 or 15 cm D_{bh}.

In this paper we present an approach for objectively estimating stem frequencies in small diameter classes (absent in stand tables) based on stem frequencies in larger diameter classes. This approach is applicable only to inventories which report all species present in the forest, and not to inventories which are limited to certain commercial subsets of species. Reliable extrapolation of truncated stand tables will greatly expand the spatial coverage of biomass estimates of tropical forests to better address their role in global biogeochemical cycles (e.g., the global carbon cycle).

In this study, we use stand tables from inventories that were based on hundreds or thousands of individual plots located over a forest of interest under some kind of formal sampling design. The unqualified term 'stand table' thus refers to the average stand table for a large forested area, rather than an individual stand or 'management unit' common to more intensely managed forests in temperate regions. We will deal only with trees in diameter classes greater than 10 cm, as this accounts for most of the biomass in a closed forest ($\geq 96\%$; Brown and Lugo, 1984).

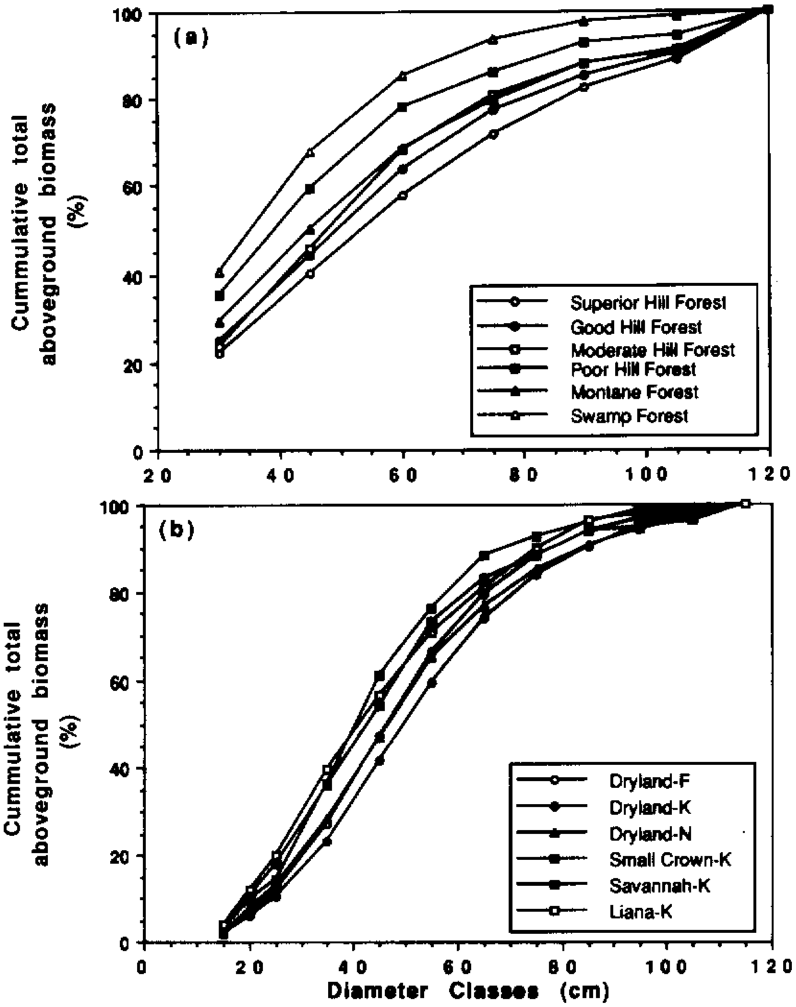

Fig. 1. Cumulative distribution of total above-ground biomass (percent) vs. the endpoint of diameter (at breast height) classes for undisturbed tropical moist forests of (a) Malaysia and (b) Surinam. The diameter classes were 15 cm wide in (a) and 10 cm wide in (b). In (b), F=Fallawatra, K=Kabalebo, and N-Nassau, three regions in Surinam where the inventories were done.

The objectives of this paper were to: (1) examine diameter distributions in primary and disturbed tropical forests; (2) test our ability to estimate numbers of stems in smaller diameter classes from numbers in larger size classes (i.e., 'complete' the stand table); and (3) test our ability to estimate the biomass contained in missing D_{bh} classes. For the purposes of this paper, 'biomass' is defined as the total above-ground dry-weight of all trees ≥ 10 cm D_{bh} and 'volume' as the standing commercial volume of all trees ≥ 10 cm D_{bh}.

METHODS

The exponential model: De Liocourt's q

We are interested in whether or not the frequency distributions of tree diameters in primary and successional tropical forests can be adequately described by a convenient mathematical function. Uneven-aged stands in temperate regions often have a characteristic exponential or 'inverse J'-shaped diameter frequency distribution, with high frequency of seedlings and saplings and gradually decreasing numbers of small and large trees. This has been found to be the case for many stands managed under the selection silvicultural system, as well as for many unmanaged natural forests (e.g., Meyer, 1952; Dawkins, 1958). This model has also been found to approximate certain even-aged stands with mixtures of shade-tolerant and intolerent trees (e.g., Smith, 1962).

The French forester De Liocourt studied the distributions of uneven-aged forests managed under the selection silvicultural system. He assumed a stand of trees grouped in $i=1$ to p D_{bh} classes of equal width, and hypothesized that the ratio of numbers of stems in adjacent diameter classes was constant, a constant commonly called De Liocourt's q:

$$q=N_i/N_{i+1} \quad i=1, 2, \dots (p-1) \tag{1}$$

where N_i is the number of trees in D_{bh} class i. This implies that the frequency distribution of diameters in p equally sized classes can be expressed as a finite geometric series of the form:

$$mq^{p-1}, mq^{p-2}, \dots mq, m=\{mq^{p-i}: i=1 \text{ to } p\} \tag{2}$$

where q is the constant ratio described above, and m is the number of trees in the largest size class. The number of trees in the D_{bh} class with midpoint D_i can be expressed by an exponential function of the form:

$$N_i=hae^{-bD_i} \tag{3}$$

where h=the width in units of the D_{bh} class, and a and b are constants relating to the shape of the diameter distribution. Since $D_{i+1}=D_i+h$, straightforward substitution of (3) into (1) implies that

$$q=e^{hb} \tag{4}$$

Distributions where b is constant over the entire range of D_i are called 'single q distributions'. When b assumes different values for different ranges of D_i, then the distribution is commonly called 'multiple q'.

The constants a and b of equation (3) are most easily comprehended after a log (ln) transformation, as is commonly done:

$$\begin{aligned}\mathrm{Ln}(N_i) &= \mathrm{Ln}(ha) - b(D_i) \\ &= b_0 + b_1 D_i\end{aligned} \tag{5}$$

Assuming sufficiently broad (5–10-cm) diameter classes, a stand of trees which conforms to this model should have diameter class frequencies such that $\mathrm{Ln}(N_i)$ plotted against D_i is approximately linear with slope b_1 and intercept b_0. For a given diameter class width h and slope b_1, the intercept b_0 is a measure of relative stand density. The slope b_1 is negative, and can vary with factors which affect survival and diameter growth, e.g. site quality, species composition, maximum attainable diameter, and stand density.

Many other models have been proposed to describe uneven-aged diameter distributions of mostly temperate forests (cf. Bailey and Dell, 1973), including a model for disturbed uneven-aged forests in New Hampshire, USA, which assumed an increasing q ratio with increasing D_{bh} classes (Leak, 1964), a model for unmanaged stands in Wisconsin, USA, that proposed a 'rotated sigmoid' distribution of $\mathrm{Ln}(N_i)$ vs. D_{bh} (Goff and West, 1975), and a multiple-q model for managed uneven-aged forests in the Lake States, USA (Eyre and Zillgitt, 1953). An example for tropical forests was the study by Wadsworth (1977), who found that a single uneven-aged forest plot of 0.4 ha did not follow a single-q model.

The Weibull distribution may be a better model for describing uneven-aged diameter distribution classes (Bailey and Dell, 1973). It is essentially a variable-q model, with the exponential model as a special case of it. The Weibull distribution works well for complete stand tables with small diameter class intervals based on many plots. We chose not to use this distribution because: (1) our main goal is to estimate missing stems in the smallest diameter classes, not necessarily to describe the diameter distributions; and (2) our data have a small number of relatively large classes, and there are statistical problems associated with fitting a curve (three parameters) to a small number of points (about 5–6).

These different models attempt to distinguish between real but subtle patterns in D_{bh} distributions which can only be noted when actual D_{bh} distributions are recorded in relatively small intervals, say 2–5-cm D_{bh} classes. However, most of the data for biomass estimation available from tropical regions consist of stand tables from large-scale forest inventories compiled in 10–15-cm D_{bh} classes. Although this could cause a grouping problem in estimation of the values of b_1, the choice in the groupings of data were beyond our control. As the foci of interest in this study are smaller diameter classes of such stand tables, we will examine the hypothesis that a single-q model is appropriate and useful for estimating numbers of trees by diameter class for the small-to-medium diameter classes.

Description of the data

We used three data sources for tropical forests growing in the moist life-zone (sensu Holdridge, 1967) in this study. The first data set came from a large scale national forest inventory of Peninsular Malaysia conducted by the Government of Malaysia in 1981–82 (Anonymous, 1987). Stand and stock tables by species were compiled for each of eleven dipterocarp forest types defined in the inventory (Table 1). The nomenclature for the undisturbed upland forests is based on their potential volume yield, which decreases in the order shown in Table 1 (superior hill forest to upper-hill/montane forest). However, these forests are not really undisturbed in the true sense of the word, because of evidence of biomass degradation in the previous ten-year period (Brown et al., 1991). Logged and disturbed forests have both been logged, but the difference between them is based on when they were logged: disturbed forests were selectively harvested prior to 1966, and logged forests were selectively harvested since 1966. This distinction originates from the time (1966) when the first set of aerial photos were taken of Malaysia for assessing their forest resources. Shifting-cultivation forests are a mixture of cleared land, secondary forest fallows of different ages, and small patches of primary forest. The stand and stock tables use 15-cm diameter classes, starting at 15 cm D_{bh}

TABLE 1

R^2 values from simple linear regressions of Ln(N) (N=number of stems per diameter class) vs.D (D_{bh} class) for 20 inventories from Peninsular Malaysia and Surinam (D_{bh} classes=6 for Malaysia and 9 for Surinam)

Malaysia[a]		Surinam[a]	
Forest type	R^2	Forest type[b]	R^2
Undisturbed Forest			
Superior hill	0.98	Dryland-N	1.00
Good hill	0.99	Dryland-F	0.99
Moderate hill	1.00	Dryland-K	0.99
Poor hill	0.99	Creek-N	0.98
Upper hill/montane	0.99	Creek-F	0.99
Freshwater swamp	1.00	Creek-K	0.96
Disturbed Forests		Small crown-K	0.96
Logged hill	0.99	Savannah-K	0.97
Disturbed hill	0.99	Liana-K	0.98
Shifting cultivation	0.96		
Logged freshwater swamp	0.99		
Disturbed freshwater swamp	0.99		

[a] Data for Peninsular Malaysia are based on the 1981–1982 National Forest Inventory (Anonymous, 1987) and, for Surinam, on a 1972–74 inventory (De Milde and Inglis, 1974a,b,c).

[b] N, Nassau; F, Fallawatra; K, Kabalebo — three regions of Surinam where inventories were done.

and continue to the 105+cm D_{bh} class. Gross commercial volume was estimated by local volume regressions (based on D_{bh} and commercial height) specifically developed as part of this inventory. We estimated total above-ground biomass of the forests by the methods and biomass regression equations reported in Brown et al. (1989).

The second data set consisted of stand and stock tables from large-scale forest inventories of undisturbed primary forest in east, central and west Surinam, conducted by the FAO in 1972–1974 (De Milde and Inglis, 1974a,b,c). Stand and stock tables were compiled by area for up to six forest types, with only the most heavily sampled forest types included in our analysis (Table 1). We use the same nomenclature for the forests as used in the original report. Dryland forests are analogous to closed-canopy upland forests; creek forests are riparian forests; and savannah, small crown, and liana forests tend to be edaphic associations and resemble open-canopy formations. Stand and stock tables use 5-cm D_{bh} classes for trees 9.5–24.5 cm D_{bh} and 10-cm classes for trees from 24.5 cm to 104.5 cm D_{bh}. We dropped the smallest diameter class (9.5–14.5 cm) and regrouped the trees from 14.5 to 24.5 cm into one D_{bh} class for part of our analyses. Local volume regression equations based on D_{bh} and commercial height were used to estimate gross commercial biomass. Total above-ground biomass was determined as reported above for Malaysia.

The third data set consisted of 28 mature forest plots in Venezuela from the personal records of J.P. Veillon, University of the Andes, Merida, Venezuela (summarized in Veillon, 1985). These records report circumference, species, and total height for some 3800 trees $\geq$ 10 cm D_{bh}. Volume was computed using equations given by Veillon (1970) and Veillon and Silva (1972). Total above-ground biomass was determined as above.

RESULTS AND DISCUSSION

Fitting of q *to stand tables from Malaysia and Surinam*

We developed the q relationship by fitting a least-squares line to equation (5) for the large-area stand tables of Malaysia and Surinam. We dropped the largest diameter class which grouped all trees above 105 cm D_{bh}, leaving six closed diameter classes through which to fit the least squares lines. As we had exactly one 'mean' point for each level of $D(=D_{bh}$ class midpoint) we had no information about the conditional variance of $\mathrm{Ln}(N)$ given D for any single forest type, so we hesitate to call this a 'regression analysis' and prefer the term 'least squares line'. The relationship was strongly linear for all forest types, with R^2 between 0.96 and 0.99 (Table 1). These results are not entirely surprising, given the few observations per forest type, but nonetheless are indicative of the strength of the linear trend. Plots of ordinary residuals showed no consistent under- or overestimation of diameter class frequencies.

A scatterplot of the regression coefficients b_0 and b_1 for the Malaysian and Surinam inventories shows the negative correlation between the coefficients: higher slopes are associated with lower intercepts, and vice versa (Fig. 2). The variation in the coefficients is indicative of the natural variation across forest types. The disturbed forest types appear to cluster at the lower end of the graph, suggesting a higher number of smaller stems and lower number of larger stems for these forest types than for undisturbed ones.

The least-squares lines for the undisturbed forest types of Malaysia show differences associated with forest type (Fig. 3). The slopes of the least-squares line become noticeable steeper going from high- (superior hill forest) to low- (poor hill forest or swamp) volume forests, indicative of the fewer number of larger trees in the lower-volume forests. In contrast, the intercepts of the undisturbed forests are similar across forest type, indicating approximately equal numbers of stems in the smaller D_{bh} classes. The least-squares lines for the forests of Surinam exhibited patterns similar to those of Malaysia.

Our analysis suggests that diameter distributions in undisturbed tropical forests in Malaysia and Surinam follow an approximate exponential distribution, at least up to the 105-cm D_{bh} class. This tends to agree with work by Dawkins (1958), who reported what he called a 'Pantropical All-Species Stand Table', a generic stand table based on his work in Africa and southeast Asia, and which also followed very closely the exponential distribution. However, our results suggest that this 'generic tropical stand table' needs to be modified according to standing stock of volume or biomass. High volume or biomass forests tend to have flatter diameter distributions, suggesting similar numbers

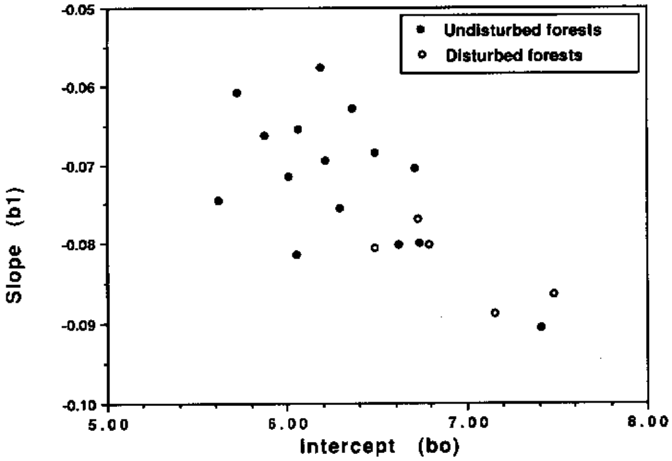

Fig. 2. Scatterplot of the regression coefficients b_0 and b_1 for the exponential model (Equation (5)) fitted to stand tables from 20 undisturbed and disturbed forest types in Malaysia and Surinam.

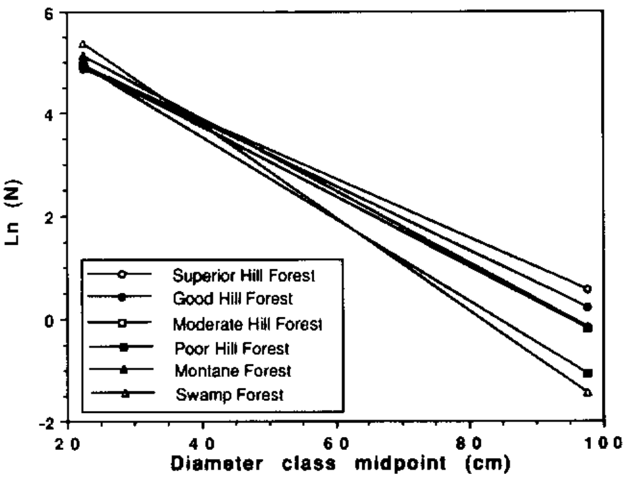

Fig. 3. Estimated least-squares lines between LnN_i (number of stems) and D (D_{bh} class midpoint) for undisturbed forest types of Malaysia, illustrating differences in slope associated with forest quality.

of small trees but relatively more large trees than lower volume or biomass forests (Fig. 3).

The disturbed, logged, and shifting cultivation forests in Malaysia also followed the exponential distribution (Table 1), with steeper slopes than the high-volume undisturbed forest (Fig. 2). The relatively good fit of the exponential model was unexpected in this case, because it was assumed that disturbance would affect the numbers of stems in larger class differently than it affects the numbers in smaller classes. The disturbed sites have fewer trees in the larger size classes than do undisturbed sites, but similar numbers in the smaller size classes. Thus, on a national scale, disturbed forests in Malaysia may also be approximated by an exponential diameter distribution.

Fitting of q *to individual-plot data*

The stand tables used above are based on large-scale forest inventories. One must consider whether the strong q relationships are scale dependent, or whether the strength of the frequency: D_{bh}-class relationship is related to the amount of forest area surveyed in compilation of the stand table.

We analyzed the diameter distributions independently for each of 28 mature tropical forest plots in Venezuela, with plot sizes ranging from 0.06 to 1.0 ha. We grouped trees into 5-cm D_{bh} classes beginning at 10 cm, and determined the number of stems N and Ln(N) for each diameter class in each plot. The distribution of Ln(N) vs D for each plot was generally linear over the smaller (< 50 cm) diameter classes which were well represented in the plot. The R^2 ranged from 0.40–0.98, with more than 75% of the plots having $R^2 > 0.75$. However, many plots had several trees which were much larger than the rest of the trees in the plot, which tended to reduce the fit of the least-squares line of Ln(N) on D when all diameter classes were included. In this case, R^2 ranged from 0.30 to 0.98, with 60% of the plots having $R^2 > 0.75$.

Although the relationship between Ln(N) and D was generally linear, the slope and intercept varied from plot to plot (Fig. 4). This is reasonable, representing the spatial variation in stand distributions resulting from variations in site and soil quality, species mixes and other environmental variables, as well as random variations in the number of stems per plot. The variation between individual plots, as expressed by the differences in ranges of the least-squares coefficients, is greater than the variation among forest types in Malaysia and Surinam (compare Fig. 4 with Fig. 2). This presents some evidence that the variation in diameter distribution is scale-dependent. Variation among individual plots may well be greater than the average differences between certain types of forests.

A combination of all 28 plots, weighted by area, resulted in a regression of Ln(N) vs D with an R^2 of 0.81 over the entire range of data (i.e., up to diameter class 212.5 cm) with the coefficients defining a point in the middle part of the scatterplot (Fig. 4). When diameter classes were limited to ≤ 50 cm, R^2 increased to 0.98. The implications of our analysis of small forest plots are: (1) forest inventories based on many plots from large areas will provide a better base for diameter distribution extrapolation than will stand tables based on individual sample plots, and that reliability of diameter distribution models depends in part upon the scale of inventory used to collect the original

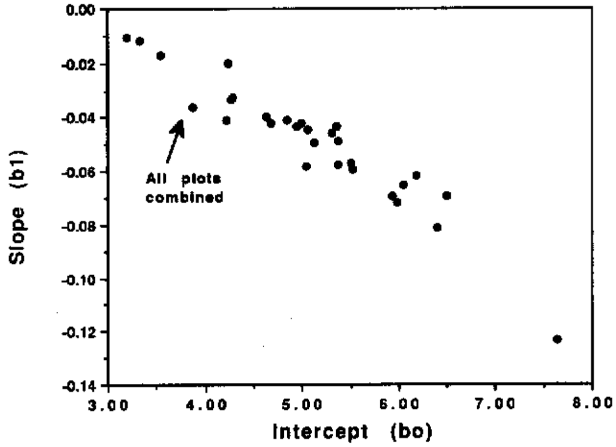

Fig. 4. Scatterplot of the regression coefficients b_0 and b_1 for the exponential model (Equation (5)) fitted to stand tables from 28 individual plots (0.06–1.00 ha in area), and the combined stand table from tropical moist forests in Venezuela.

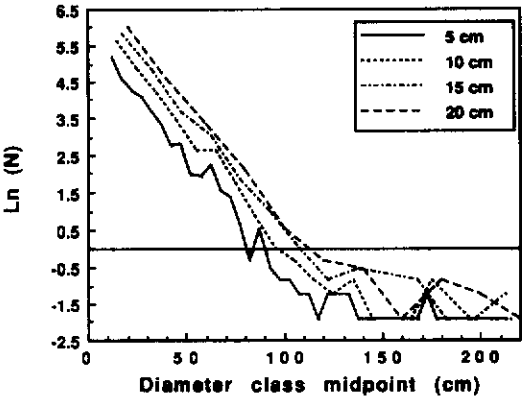

Fig. 5. Ln N_i (number of stems) vs. D (D_{bh} class midpoint) for the combined plots of Venezuela. Lines represent distributions associated with diameter classes of different widths, and shows the smoothing associated with increased diameter class sizes. The reference line at $\mathrm{Ln}(N) = 0$ shows where $N = 1$ tree/unit area.

data; and (2) the single-q exponential model is more appropriate for the small-to-medium-sized diameter classes (our goal), and a multiple-q distribution or some other function is likely needed to adequately model entire diameter distributions.

We used the Venezuelan data to consider the effect of width of the diameter class upon the smoothness of diameter distributions. We created four different diameter distributions by placing each tree into diameter classes, 5, 10, 15, and 20 cm in width, all starting at 10 cm. The diameter distribution for these combined plots is distinctly two-q, with a high q from 10 to 110 cm D_{bh} and a lower $q > 110$ cm D_{bh} (Fig. 5). The distribution also becomes smoother as diameter class width increases. This illustrates that, while it may be very difficult to estimate frequencies of larger trees, it may be feasible to estimate frequencies of smaller trees even when the diameter classes are fairly broad.

A least-squares line of Ln (N) vs D for the diameter classes below 110 cm for each of the four diameter class widths given above demonstrated that, as width increased, so did the intercept (5.7–7.4). However, the slopes remained essentially unchanged (-0.066 to -0.072). If the slope is constant over a variety of diameter class widths, it should be possible to compute different q values for a given diameter distribution using several different diameter class widths (h) and Equation (4). This might allow extrapolation of a diameter distribution in the case where diameter classes making up the stand table are not of a uniform width, e.g., if small trees are reported in 5-cm classes and larger trees in 15-cm classes.

Biomass distributions by diameter class

The models we propose in this paper use extrapolation of a least-squares line to estimate numbers of stems in missing small D_{bh} classes. Extrapolation beyond the domain of the model-generating data is known to be dangerous, possibly leading to serious bias if the model does not adequately reflect the underlying process. We therefore wish to define a 'reasonable range' of numbers of stems or proportions of volume or biomass contained in the size classes of interest, to act as a guard against unreasonable extrapolations. Thus, some consideration of the cumulative distributions of commercial volume and total above-ground biomass as a function of diameter class is appropriate.

Although trees in the smallest diameter classes have the highest frequencies in a typical uneven-aged stand, they also have the lowest individual volume and biomass. It may be questioned whether it is worth the trouble to include these trees in estimates of total stand volume and biomass. This depends on the purpose of the inventory. If the inventory is aimed at quantifying certain classes of merchantable products which require large trees, such as sawtimber or veneer stock, then the smaller trees are relevant mainly in terms of their

TABLE 2

Percent of total commercial volume and above-ground biomass contained within the smallest D_{bh} classes for tropical moist forests in Malaysia, Surinam, and Venezuela.

Data source	D_{bh} class (cm)	Percent of stand totals for:	
		Commercial volume	Above-ground biomass
Malaysia — undisturbed forest			
Superior hill	15–30	29.9	22.2
Good hill	15–30	35.4	25.1
Moderate hill	15–30	32.7	24.1
Upper hill	15–30	41.3	29.4
Poor hill	15–30	45.7	35.4
Freshwater swamp	15–30	52.9	40.6
Malaysia — disturbed forest			
Logged hill	15–30	42.3	34.6
Disturbed hill	15–30	41.5	32.3
Shifting cultivation	15–30	48.1	35.7
Logged swamp	15–30	53.8	42.5
Disturbed swamp	15–30	49.2	38.0
Surinam — undisturbed forest			
Dryland-N	10–35	28.6	28.5
Dryland-F	10–35	28.0	27.5
Dryland-K	10–35	24.0	23.3
Creek-N	10–35	29.7	29.0
Creek-F	10–35	27.5	26.5
Creek-K	10–35	29.3	26.3
Small crown-K	10–35	41.4	36.2
Savannah-K	10–35	38.9	36.4
Liana-K	10–35	42.6	39.6
Venezuela – mature forests	10–35	25.9	29.7

future potential to grow to the desired size classes. However, smaller trees may be very relevant for other merchantable products such as pulpwood, fuelwood, charcoal, or posts. In ecological studies of, for example, ecosystem productivity or carbon storage, all biomass is relevant, regardless of its dimensions.

We examined cumulative distributions of volume and biomass for our three data sources (Table 2). Our data from undisturbed moist forests in Surinam and Venezuela indicate that trees between 10 and 35 cm D_{bh} constitute 24–43% of the commercial volume and 23–40% of the above-ground biomass for all trees > 10 cm D_{bh}. Trees between 15 and 30 cm D_{bh} in undisturbed moist forests in Malaysia contain similar ranges for trees > 15 cm D_{bh}, with slightly higher values for disturbed forests (Table 2).

The proportion of volume and biomass in the smaller D_{bh} classes appears to be related to total forest volume or biomass. High-biomass forests (e.g., superior hill forests in Malaysia and dryland forests in Surinam) contained relatively more larger trees, so that lower proportions of volume and biomass were contained within the smallest D_{bh} classes (Fig. 1). In contrast, low-biomass forests such as the savannah, small crown, and liana forest in Surinam and the swamp and poor hill forests in Malaysia, tended to have higher proportions of volume and biomass in the lower D_{bh} classes.

For inventories with minimum diameters other than 35 cm, the limits on the biomass within missing diameter classes may be approximated using Fig. 1. In the absence of more site-specific information, these proportions may serve as crude limits to the minimum and maximum percent of total biomass and volume 'missing' from stand tables.

Estimation of stem frequencies and biomass in small diameter classes in Surinam forests

Given that we accept the single-q approximation of diameter distributions for small and intermediate diameter classes in undisturbed tropical forests, we wish to test whether or not some form of the model may be used to extrapolate backwards to estimate the number of missing stems in the smallest diameter classes. We tested this for nine stand tables from Surinam by dropping the 14.5–24.5 cm and 24.5–34.5 cm classes, and attempted to estimate the number of stems in the dropped classes from the number of stems in the remaining diameter classes. Here we compare the estimated and actual reported stem frequencies, as well as biomass estimates based on these frequencies.

We considered three methods for estimating the number of stems in the 'missing' diameter classes. Under Method I, we fit a least-squares line to the $\mathrm{Ln}(N)$-D relationship based on all close-ended diameter classes in the stand table — in this case seven classes with midpoints ranging from 39.5 to 99.5

TABLE 4

Comparison of reliability of Method I, II, and III estimates of total above-ground biomass of trees in the 15–35-cm D_{bh} classes for the forests of Surinam

	Dryland-N	Dryland-F	Dryland-K	Creek-N	Creek-F	Creek-K	Small Crown-K	Savannah-K	Liana-K
Total above-ground biomass (t ha^{-1}) in the 15–35-cm D_{bh} classes[a]									
Actual	71.38	66.40	52.61	68.63	52.65	55.07	45.38	65.22	39.63
Estimated									
Method I	84.21	111.83	78.90	153.02	80.71	123.76	61.14	61.51	36.43
Method II	91.41	98.66	73.96	131.98	76.63	93.24	46.95	123.05	28.59
Method III	68.79	71.21	61.54	87.78	67.32	57.72	30.32	122.06	31.47
Percent of total stand biomass assumed to be contained within the 'missing' D_{bh} classes									
Actual	27.6	26.4	22.3	28.3	25.4	26.2	35.2	35.2	38.0
Estimated[b]									
Method I	31.0	37.7	30.1	46.9	34.3	44.3	42.2	33.8	36.0
Method II	32.8	34.8	28.8	43.2	33.1	37.5	35.9	50.6	30.7
Method III	26.8	27.8	25.2	33.6	30.3	27.1	26.6	50.4	32.7
Estimated percent error (estimated-actual biomass as a proportion of known total stand biomass)									
Error of omission[c]	27.6	26.4	22.3	28.3	25.4	26.2	35.2	35.2	38.0
Method I	5.0	18.1	11.2	34.9	13.5	32.6	12.2	−2.0	−3.1
Method II	7.7	12.8	9.1	26.2	11.6	18.1	1.2	31.2	−10.6
Method III	−1.0	1.9	3.8	7.9	7.1	1.3	−11.7	30.7	−7.8
Estimated percent error using bounds of 20–40% on the percent of biomass allowed in 'missing' classes									
Error of omission[c]	27.6	26.4	22.3	28.3	25.4	26.2	35.2	35.2	38.0
Method I	5.0	18.1	11.2	19.4	13.5	23.1	8.1	−2.0	−3.1
Method II	7.7	12.8	9.1	19.4	11.6	18.1	1.2	8.0	−10.6
Method III	−1.0	1.9	3.8	7.9	7.1	1.3	−11.7	8.0	−7.8

[a] Biomass in the 15–35-cm classes is taken as the sum of (# stems in 15–35-cm classes) $*$ (biomass of tree of D_{bh} = class midpoint), where biomass is computed using the moist forest equation in Brown et al. (1989).

[b] (Estimated biomass in the 'missing' classes) / (estimated biomass in the 'missing' classes + known biomass in the present classes).

[c] The error resulting if the trees < 35 cm D_{bh} are ignored.

The difference between the estimated and actual biomass of the missing D_{bh} classes, as a percent of the known total stand biomass, indicates the error associated with estimating (rather than ignoring) stems in the missing diameter classes under the respective method (Table 4). The error of omission is always greater than the error associated with Methods II and III, and is greater in seven out of nine cases for Method I. As with stem frequencies, Method III appears to give the best results for the forests of Surinam, particularly for the higher-biomass forests.

We can improve our biomass estimation by using the limits discussed earlier to eliminate unreasonably large or small estimates of biomass for the missing diameter classes. We forced the estimated biomass of trees 15–35 cm to be at least 20% but no more than 40% of the total stand biomass. If we replace the estimates which are too high or too low, then the percent errors range between −2 and 23%, −11 and 19%, and −12 and 8% for Methods I, II, and III respectively, with all errors less than the error of omission. These limits and estimates may be further refined by additional consideration of the relationship between biomass distribution and total stand biomass, using lower limits for higher-biomass stands, and vice versa. Although the example above uses biomass as a check on the success of estimation of stem frequency, the same approach could be taken with volume. If one were interested in stem frequencies themselves, the percent reduction in biomass or volume could be applied to reduce the estimate of the stem frequencies.

Although Method III is derived by consideration of the exponential diameter-distribution model, the method could be treated as a simple ratio-estimator problem where the ratio of interest is that of the numbers of stems in the smallest two present diameter classes. Using methodology described by Cochran (1977) or Cunia (1985), point and interval estimates for the ratio and for the number of stems in the missing diameter classes could be derived. This approach would require data not generally reported with stand tables, such as estimates of means, variances, and covariances of numbers of stems in the diameter classes.

CONCLUSIONS

This study uses data mostly from tropical moist forest life-zones (sensu Holdridge, 1967), but the approaches described may also work in other life-zones. The model of stand distributions discussed in this paper is primarily developed for research purposes to obtain estimates of total above-ground biomass for forests where inventory information is for trees greater than some large commercial limit. However, the model may be suitable for other purposes, e.g., commercial inventory extrapolation for planning purposes or development of optimum stand tables (targets) for tropical moist forest management under an uneven-aged silvicultural system.

Although these methods are not as accurate as direct observation of stem frequencies, for many applications they are better than just ignoring trees below some large commercial limit which are an important proportion of the total stand biomass or volume. This error of omission may be substantial, regardless of the total biomass of the forest.

A user of this method should use local forest information or the discussion in the earlier section on biomass distributions to modify the decision rule for cases where other diameter limits apply. When the minimum diameter of the stand table is other than the 35 cm used in the above example, the user will have to determine other limits on the expected proportion of total stand biomass contained in the missing diameter classes. In the absence of better information, Fig. 1 might be one source of approximating the limits.

Once stem frequencies have been estimated, completed stand tables may be used for other purposes such as volume and biomass estimation. We have applied this method of stand table completion (using Method III) to several inventories of forests in tropical Asia and America to estimate their aboveground biomass (Brown et al., 1991 and Brown, unpublished data). This has expanded our forest biomass data base for developing biomass maps for use in spatial models of the tropical terrestrial carbon cycle.

Several of our results indicate that the exponential distribution applies to disturbed as well as to undisturbed tropical forests; however, the issue of scale must be considered. Disturbed-forest stand tables considered in this paper came from large areas which had been disturbed over a long period of time. It is unlikely that residual forests on a smaller area (such as a single harvest site) or a large area that had been disturbed at one time (such as the undisturbed forest area cut in one season of logging) would follow an exponential diameter distribution. The approaches described in this paper are most applicable to forest inventories of very large areas.

ACKNOWLEDGEMENTS

We thank Thang Hooi Chiew of the Government of Malaysia, and K.D. Singh of the UN Food and Agriculture Organization, Rome, Italy, for help in locating suitable forest inventories for use in this study; Jean-Pierre Veillon of Universidad de los Andes, Merida, Venezuela for providing the data on forest plots; W.B. Smith for helpful comments on an earlier draft of this paper; and R. Nyland who reviewed an early draft of this manuscript and made numerous helpful comments as well as a suggestion leading to the Method III. This research was performed under subcontract 19X-SB832C with S. Brown at the University of Illinois and 19X-43326C with A.E. Lugo at the Center for Energy and Environment Research, University of Puerto Rico, under Martin Marietta Energy Systems Inc. contract DE-ACO5-840R21400 with the U.S. Department of Energy.

REFERENCES

Anonymous, 1987. Inventori Hutan Nasional II Semenanjung Malaysia 1981–1982. [National Forest Inventory of Peninsular Malaysia 1981–1982] Unit Pengurusan Hutan, Ibu Pejabat Perhutan, Semenanjung Malaysia, Kuala Lumpur, 201 pp.

Bailey, R.L. and Dell, T.R., 1973. Quantifying diameter distributions with the Weibull function. For. Sci., 19: 97–104.

Brown, S. and 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. and Lugo, A.E., 1984. Biomass of tropical forests: a new estimate based on forest volumes. Science, 223: 1290–1293.

Brown, S., Gillespie, A.J.R. and Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. For. Sci., 35: 881–902.

Brown, S., Gillespie, A.J.R. and Lugo, A.E., 1991. Biomass of tropical forests of South and Southeast Asia. Can. J. For. Res., 21: 111–117.

Cannell, M.G.R., 1982. World Forest Biomass and Primary Production Data. Academic Press, London, 391 pp.

Cochran, W.G., 1977. Sampling Techniques (3rd edition). Wiley, New York, 428 pp.

Cunia, T., 1985. More basic designs for survey sampling: two-stage and two-phase sampling, ratio and regression estimators and sampling on successive occasions. Faculty of Forestry, State Univ. NY, Coll. Environ. Sci. For., For. Biometry Monogr., 4: 368 pp.

Dawkins, H.C., 1958. The management of natural tropical high-forest with special reference to Uganda. Imp. For. Inst., Univ. Oxford, Pap., 34: 155 pp.

De Milde, R. and Inglis, C.J., 1974a. Forestry development in Surinam, inventory of the Fallawatra area. FAO, Paramaribo, Proj. Work. Doc., 7; 41 pp.

De Milde, R. and Inglis, C.J., 1974b. Forestry development in Surinam, inventory of the Nassau area. FAO, Paramaribo, Proj. Work. Doc., 8; 42 pp.

De Milde, R. and Inglis, C.J., 1974c. Forestry development in Surinam, inventory of the Kabalebo area. FAO, Paramaribo, Proj. Work. Doc., 9; 69 pp.

Eyre, F.H. and Zillgitt, W.M., 1953. Partial cuttings in northern hardwoods of the lake states. USDA For. Serv., Lake States For. Exp. Stn., Tech. Bull., 1056.

Goff, F.G. and West, D., 1975. Canopy-understory interaction effects on forest population structure. For. Sci., 21: 98–108.

Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica, 206 pp.

Johnson, W.C. and Sharpe, D.M., 1983. The ratio of total to merchantable forest biomass and its application to the global carbon budget. Can. J. For. Res., 13: 372–383.

Leak, W.B., 1964. An expression of diameter distributions for unbalanced, uneven-aged stands and forests. For. Sci., 10: 39–50.

Meyer, H.A., 1952. Structure, growth and drain in balanced unevenaged forests. J. For., 50: 85–92.

Smith, D.M., 1962. Principles of Silviculture (7th edition). Wiley, New York, 578 pp.

Veillon, J.P., 1970. Tablas de cubicacion de rolas, tablas de volumen para arboles en pie y tablas de produccion de plantaciones forestales. Instituto de Silvicultura, Seccion de Ordinacion de Forestal, Facultad de Ciencias Forestales, Universidad de los Andes, Merida, Venezuela.

Veillon, J.P., 1985. El crecimiento de algunos bosques naturales de Venezuela en relacion con los parametros del medio ambiente. Rev. For. Venez., 29.

Veillon, J.P. and Silva, R., 1972. Tablas de volumen para arboles en pie y tablas de produccion de plantaciones forestales en la America Latina. Instituto de Silvicultura, Seccion de Ordinacion de Forestal, Facultad de Ciencias Forestales, Universidad de los Andes, Merida, Venezuela.

Wadsworth, R.K., 1977. A study of diameter distributions of an uneven aged tropical forest by means of a transition matrix model. Ph.D. dissertation, University of Washington, Seattle, 156 pp.

je_iitf_1992_gillespie001