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4 March 1983; accepted 22 July 1983

Biomass of Tropical Forests: A New Estimate Based on Forest Volumes

Abstract. *Recent assessments of areas of different tropical forest types and their corresponding stand volumes were used to calculate the biomass densities and total biomass of tropical forests. Total biomass was estimated at 205 × 10⁹ tons, and weighted biomass densities for undisturbed closed and open broadleaf forests were 176 and 61 tons per hectare, respectively. These values are considerably lower than those previously reported and raise questions about the role of the terrestrial biota in the global carbon budget.*

The recent rise in atmospheric CO_2 concentration (*1*) due to the burning of fossil fuels and its potential effects on climate have renewed interest in the study of the global carbon cycle. Of particular interest is the attempt to balance the world's carbon budget and account for all known sinks and sources (*2*). At the present the budget appears to be unbalanced because of a proposed source of CO_2 from the terrestrial biota, estimated by Houghton *et al.* (*3*) as per 1.8×10^9 to 4.7×10^9 tons of carbon per year for 1980. Most of this proposed net flux from the biota (~ 80 percent) is due to changes in land use in the tropics.

The uncertainty in the magnitude of the flux due to tropical deforestation results partly from uncertainty in the estimates of the biomass density (or organic carbon density, as mass per unit area) of tropical forests and the rate of deforestation. The carbon densities of tropical forests commonly used in models of the terrestrial biota (*3, 4*) are those of Whittaker and Likens (*5*) and of our earlier study (*6*). Whittaker and Likens' study recognized two forest types with carbon densities of 160 to 200 ton/ha, giving a total carbon pool of 460×10^9 tons (or a weighted carbon density of about 188 ton/ha). In our study, we recognized six forest types with carbon densities of 40 to 185 ton/ha, giving a total carbon pool in tropical forests of 228×10^9 tons (or a weighted carbon density of 124 ton/ha). The two weighted carbon densities differ by a factor of 1.5. Other estimates of the weighted carbon density of tropical forests are 114 ton/ha (*7*) and 165 ton/ha (*8*).

Table 1. Ratio of total biomass to wood biomass for a variety of tropical forests.

Life zone	Biomass (ton /ha)		Ratio of total biomass to stemwood biomass	Reference
	Stemwood	Total		
Tropical premontane wet forest	416.1	689.7	1.7	(*12*)
	272.8	475.3	1.7	(*12*)
Tropical lower montane rain forest	385.0	552.8	1.4	(*13*)
Tropical montane wet forest	269.7	415.8	1.5	(*26*)
	269.7	374.0	1.4	(*27*)
Tropical wet forest	229.5	415.2	1.8	(*28*)
	201.3	348.0	1.7	(*28*)
	110.5	171.7	1.6	(*28*)
	297.0	501.3	1.7	(*12*)
Tropical moist forest	346.0	473.7	1.4	(*29, 14*)
	297.5	394.3	1.3	(*15*)
	298.9	473.1	1.6	(*15*)
	206.0	324.2	1.6	(*30*)
	230.0	361.8	1.6	(*16*)
Tropical premontane moist forest	63.5	170.3	2.7*	(*15*)
Subtropical wet forest	153.3	271.8	1.8	(*31*)
Subtropical moist forest	135.0	230.4	1.7	(*15*)
	209	290.8	1.4	(*16*)
	112	157.0	1.4	(*16*)
Subtropical dry forest	55	78.1	1.4	(*16*)
	29.0	89.8	3.1†	(*32*)
Mean (standard error)			1.6 (0.04)	

*Not included in the calculation of the mean because these two forests are typical of open forest formations. Trees in this formation tend to branch more and have a larger proportion of their biomass in branches and below ground.

The data base for estimating the biomass or carbon pool in tropical forests is poor at best (*6*). The few studies in which the biomass of tropical forests has been measured by destructive sampling cover only a small area (< 30 ha). They also tend to be concentrated in a few forest life zones [10 out of 33, as defined by Holdridge (*9*)], while other life zones, particularly the very wet and very dry, have barely been studied.

In contrast, much more information on standing timber volumes in tropical forests from a broader geographical area and from more and larger plots is available. We now present our derivation of another estimate of the total biomass or carbon pool and weighted biomass density of tropical forests based on volumes of forest stands. For this new estimate we used data from the recent reports of the Food and Agriculture Organization (FAO) (*10*). These reports give detailed information on forest areas and corresponding stand volumes within the tropical regions of America, Africa, and Asia, country by country. Seventy-six countries were surveyed, covering 97 percent of the area that lies in the tropical belt.

There are two major forest categories according to the FAO study: closed forests in which the forest stories cover a high proportion of the ground and lack a continuous dense grass cover and open forests in which the mixed broadleaf-grassland tree formation has a continuous dense grass layer and the tree canopy covers more than 10 percent of the ground. The former may be dominated by broadleaf (evergreen, deciduous, or semi-deciduous) or coniferous species growing in wet, moist, or dry climates. Within these two broad classes of forest types there are further classifications according to degree of disturbance, productiveness, or unproductiveness (see Table 2, notes).

To estimate the biomass for tropical forest vegetation, we used the volume and area data in the FAO reports (*10*). Stand volume is defined as the gross volume over bark (VOB) of the free bole (from stump to crown point or first main branch, generally to a top diameter of 7 cm) for all living trees with a diameter at breast height ≥ 10 cm. In general, the

FAO data of forest volumes were derived from inventories that covered large forest areas, and they represent weighted averages to account for different forest types within a given forest category.

We used the wood densities for about 380 tropical trees reported in Chudnoff (*11*) to convert VOB to biomass (defined as stemwood biomass). We calculated a mean density for both broadleaf and coniferous species for each of the three tropical regions. There was little difference in mean wood densities (tons per cubic meter ± standard error) among the three tropical regions for either broadleaf species (America, 0.62 ± 0.01, $N = 146$; Africa, 0.58 ± 0.01, $N = 106$; Asia, 0.57 ± 0.01, $N = 100$) or coniferous species (America, 0.46 ± 0.02, $N = 6$; Africa, 0.45 ± 0.01, $N = 3$; Asia, 0.52 ± 0.06, $N = 7$).

To determine a suitable factor for converting stemwood biomass to total biomass (above and below ground) of the stand we used information from studies covering a range of life zones and thus forest types that measured directly (destructive sampling) the total biomass of tropical forests broken down by individual components. These components included stemwood, branches, leaves, and roots. Biomass of the understory was not included because very few studies measured this. In general, however, it accounts for less than 2 percent of the total biomass of closed forest formations (*12–16*). The ratios of total biomass to stemwood biomass varied slightly with life zone (Table 1), but not significantly (analysis of variance, $P = 0.05$). The mean ratio of total biomass to stemwood biomass of 1.6 (Table 1) is identical to the value proposed by Dawkins (*17*).

To estimate the total forest biomass from stemwood biomass, we applied the ratio of 1.6 to the closed forest category. A ratio of 3 was used to convert stemwood biomass of open forest formations to total biomass, based on the two values in Table 1. Both of these ratios, however, are based on undisturbed forests, and it is possible that for the logged or unproductive forests they may be conservative.

A summary of the forest areas, volumes, and biomass values for the various forest groups, based on FAO data and classifications, is given in Table 2. The total forest area is 1.929×10^9 ha, of which 62 percent is closed forest. Total volume-derived biomass for tropical forests is about 205×10^9 tons or 102×10^9 tons of carbon (assuming 1 ton of organic matter is equivalent to 0.5 ton of organic carbon), giving an average carbon density for tropical forests of 53 ton/ha. This new estimate is considerably lower than

Table 2. Biomass of tropical forests based on volume estimates (areas and volumes from *10*).

	Closed forests*							Open forests†		
	Broadleaf			Conifer			Total	Productive‡	Unproductive‖	Total
	Undisturbed-productive‡	Logged§	Unproductive‖	Undisturbed-productive‡	Logged§	Unproductive‖				
Tropical America										
Area (10^6 ha)	452.98	53.50	147.45	1.53	13.64	9.56	678.66	142.89	74.11	217.00
Volume (10^9 m^3)	71.07	6.37	13.21	0.27	0.93	0.63	92.48	6.17	1.33	7.50
Stemwood biomass (10^9 tons)¶	43.92	3.94	8.19	0.13	0.43	0.29	56.90	3.81	0.82	4.63
Total biomass (10^9 tons)*	70.28	6.31	13.10	0.21	0.69	0.47	91.06	11.02	2.47	13.49
Biomass density (ton/ha)	155.1	117.9	88.8	136.0	50.4	49.2		77.1	33.3	
Tropical Africa										
Area (10^6 ha)	118.18	43.57	52.66	0.27	0.31	0.54	215.53	169.22	317.23	486.45
Volume (10^9 m^3)	30.3	8.41	7.35	0.05	0.02	0.07	46.21	4.68	3.76	8.44
Stemwood biomass (10^9 tons)¶	17.56	4.87	4.26	0.02	0.01	0.03	26.75	2.71	2.18	4.89
Total biomass (10^9 tons)#	28.09	7.79	6.82	0.03	0.02	0.05	42.80	7.83	6.54	14.37
Biomass density (ton/ha)	237.7	178.9	129.5	118.5	51.6	88.9		46.3	20.6	
Tropical Asia										
Area (10^6 ha)	97.26	94.62	100.08	1.77	3.83	2.80	300.36	8.53	22.42	30.95
Volume (10^9 m^3)	20.97	9.70	14.45	0.30	0.52	0.35	46.29	0.41	0.35	0.76
Stemwood biomass (10^9 tons)¶	11.93	5.51	8.24	0.16	0.27	0.18	26.29	0.23	0.20	0.43
Total biomass (10^9 tons)#	19.09	8.82	13.18	0.26	0.43	0.29	42.07	0.67	0.59	1.26
Biomass density (ton/ha)	196.3	93.2	131.7	144.9	112.5	103.6		79.0	26.32	
Total Tropics										
Area (10^6 ha)	668.42	191.69	300.19	3.57	17.78	12.90	1194.55	320.64	413.76	734.4
Volume (10^9 m^3)	122.35	24.48	35.01	0.62	1.47	1.05	184.98	11.26	5.44	16.70
Stemwood biomass (10^9 tons)¶	73.41	14.32	20.69	0.31	0.71	0.50	109.94	6.75	3.20	9.95
Total biomass (10^9 tons)#	117.46	22.92	33.10	0.50	1.14	0.81	175.93	19.52	9.60	29.12
Weighted biomass density (ton/ha)	175.7	119.6	110.3	140.1	64.1	62.8	147.3	60.9	23.2	39.7

*Closed forests are those whose forest stories cover a large proportion of the ground and lack a continuous dense grass layer. They may be evergreen, semi-deciduous, or deciduous, and wet, moist, or dry. †Open forests are mixed broadleaf-grassland tree formations with a continuous dense grass layer, and the tree canopy covers more than 10 percent of the ground. It is an ecological rather than physiognomic distinction, and in some cases the trees can cover the ground completely as with a closed forest. ‡Primary (virgin) or old secondary forests where there has been no logging for more than 60 years but which contain trees suitable for the wood industry. §Forests selectively harvested one or more times during last 60 to 80 years. This category also includes intensively managed forests. ‖Unproductive forests due to physical reasons (for example, poor form, rough terrain, or flooded) or legal reasons (for example, national parks or reserves). We used the volumes (m^3/ha) for the undisturbed productive forests to calculate biomass of the legally unproductive forests because national parks and reserves usually include high-volume tropical forests. However, the area in national parks and reserves accounted for about only 13 percent of the total unproductive category. ¶Calculated as the product of volume and average wood density by species group and region. #Product of stemwood biomass × 1.6 (from Table 1) for closed forests; product of stemwood biomass × 3.0 (average of the two values for open forests in Table 1) for open forests.

the values of 124 tons of carbon per hectare from our earlier study (*6*) or 188 tons of carbon/ha from Whittaker and Likens (*5*).

The low weighted, volume-derived biomass density of closed forests (176 ton/ha) does not imply that volumes for all tropical forests were equally as low. In fact, the higher values for volume-derived biomasses of some tropical humid forest areas are similar to the biomass values we used earlier (335 ton/ha) and those used by Whittaker and Likens (375 ton/ha). For example, the volume-based estimates for tropical closed forests of the Cameroons, Congo, and Ivory Coast ranged from 221 to 355 ton/ha. The mixed dipterocarp forests of insular Asia gave biomass estimates of about 250 to 300 ton/ha. In the Asia forest case, some may believe that even these high-end biomass values are low because volumes as high as 750 to 850 m^3/ha have been reported for these same dipterocarp forests on the basis of small sample areas (*18, 19*). The highest volume-derived biomasses for tropical America ranged from 190 to 300 ton/ha, somewhat lower than those of tropical Africa and Asia.

There are two major causes for the large discrepancy between our new estimate and the previous ones. The previous estimates assumed (i) that all tropical forests were undisturbed and, presumably, productive (as defined by the FAO), and (ii) that biomass estimates based on direct measurements of small areas of a few tropical forest types could be extrapolated to all tropical forests.

The first assumption does not apply to the open forests. According to the data from the FAO reports (*10*), most (56 percent) of the open forests are classified as unproductive with a correspondingly lower biomass density (Table 2). The second assumption, however, appears to apply, more or less, to the productive open forests. For example, the weighted biomass density of the productive open forests of 61 ton/ha (Table 2) is within one standard error of the mean of 80 ton/ha used in our earlier study (*6*). It appears, therefore, that for the undisturbed, productive open forests, volume-derived estimates of biomass density are comparable to those obtained from direct methods.

Neither of the above assumptions applies to the closed broadleaf forests (the coniferous forests will not be treated separately because these were not so considered in the previous studies, and they cover less than 3 percent of the total closed forest area). With regard to the first assumption, it is evident from Table 2 that only about 58 percent of all broadleaf forests are undisturbed, and all these are not necessarily primary forests (*20*). Of the remainder, 26 percent are unproductive and 16 percent have been logged. The biomass density of the logged forests is about 75 percent that of the undisturbed forests in tropical America and Africa but less than 50 percent of those in tropical Asia, reflecting the more intensive use of these forests (particularly the dipterocarp forests in insular Asia). The unproductive forests appear to have a biomass density that is about two-thirds that of the productive ones. These forests include various types of unique associations located in many of the forest life zones, such as the dwarf forests on many mountain tops, heath-type forests of parts of tropical Asia and America, and peat and other swamp forests. Some of the unproductive forests are classified as such because they are in national parks or reserves, about 13 percent of the total unproductive forest area. We believe that these forests have high biomass density values and have treated them as such (see footnotes to Table 2).

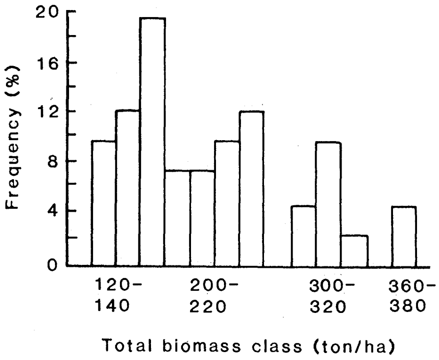

Fig. 1. Frequency distribution of total volume derived biomass, in 20 ton/ha increment size classes, for 1-ha plots covering a total area of 1230 ha of the Amazon basin (*21–23*). Original data included merchantable volume for trees of minimum diameter at breast height of 25 cm and wood densities. Total biomass = volume × wood density × 1.6 (Table 1) × 1.2 (*22*) (to account for trees down to the 10-cm-diameter class).

The second assumption does not apply to closed forests because volume-derived biomass estimates made over large areas tend to be more representative than estimates based on small areas, that is, low biomass forests are more frequent than high ones. For example, Fig. 1 shows a frequency distribution of volume-derived biomasses for tropical moist forests in the Amazon. The data were collected from many 1-ha plots located along transects hundreds of kilometers long across the Amazon Basin (*21–23*) for a total sample area of about 1230 ha. More than 50 percent of the area covered by this survey had biomass values less than 200 to 220 ton/ha (Fig. 1). Biomasses of tropical American moist forests obtained from destructive sampling methods range from 209 to 481 ton/ha (*6*), of which 50 percent have values between 209 and 330 ton/ha and the other 50 percent were between 370 and 481 ton/ha, with a higher frequency at the top end of the range. Clearly, biomasses obtained by direct measurement are not average for the Amazonian tropical moist forests but bias the sampling to the larger biomass plots. Similarly, for the tropical Asian and African moist forests, direct measurement of biomass gives values of 349 to 474 and 359 to 538 ton/ha, respectively (*6*), compared to volume-derived biomasses of 250 to 300 and 221 to 350 ton/ha, respectively.

There are four main sources of errors in this new estimate based on volumes: wood densities, expansion factors, forest areas, and stand volumes. A change in the wood densities by 1 standard error changes the weighted carbon density by only 2 percent. The effect of changing the expansion factor for closed forests by 1 standard error (from Table 1) amounts to 2.5 percent. Therefore, the uncertainty in the estimate due to these two variables is minimal. Even if the expansion factor for closed forests was as high as 2.2 (the average value for U.S. temperate hardwood forest), the figure proposed by Johnson and Sharpe (*24*), the weighted carbon density for undisturbed, closed broadleaf forests would be 121 ton/ha, still a comparatively low value compared to 168 to 188 ton/ha given for similar forests types (*5, 6*).

The uncertainties in the estimates of forest areas and stand volumes were not given in the FAO reports (*10*). The uncertainties in these values vary randomly and according to the countries and items concerned. The amount of information used to arrive at the estimates was considerable and of diverse origins, and an estimate of the variance in the data would have been subjective and arbitrary (*20*).

Regardless of any source of error, this new estimate of the weighted carbon density of all tropical forests (53 ton/ha) is well outside the range of 124 ± 25 tons of carbon per hectare proposed earlier (*6*). The range of uncertainty we estimated then was based on 2 standard errors of the biomass data, from direct harvest methods only. We did not estimate an error factor related to the uncertainty in the tropical forest area; however, the forest area we used was comparable to that used by the FAO (*10*).

The immediate implication of the lower carbon storage in tropical forests is that less carbon would be released as CO_2 when tropical forests are burned or destroyed. Using the forest carbon densities of Whittaker and Likens and our earlier study and the FAO clearing rates (*10*), Detwiler *et al.* (*4*) estimated that the net flux of carbon to the atmosphere from tropical closed forests ranges from 0.68 to 0.74 × 10^9 ton/year for 1980. This flux would be reduced by approximately half if the lower volume-derived carbon densities were used (*25*). A lower carbon flux from the tropics would enable the global carbon budget to be almost balanced.

SANDRA BROWN
Department of Forestry,
University of Illinois, Urbana 61801
ARIEL E. LUGO
Institute of Tropical Forestry,
Southern Forest Experiment
Station, Post Office Box AQ,
Rio Piedras, Puerto Rico 00928

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33. Supported by a grant from the U.S. Department of Energy, CO_2 Research Division, contract AS05-78EV6047. We thank Jean-Paul Lanly of the Forest Resources Division of the Food and Agriculture Organization in Rome and Charles Hall, Ralph Schmidt, and Ana Maria Vera for their contributions.

12 September 1983; revised 4 January 1984

Transformation and Cytopathogenic Effect in an Immune Human T-Cell Clone Infected by HTLV-I

Abstract. *Human T-cell leukemia-lymphoma virus (HTLV) is a human C-type retrovirus that can transform T lymphocytes in vitro and is associated with certain T-cell neoplasms. Recent data suggest that, in the United States, patients with acquired immunodeficiency syndrome (AIDS), homosexual men with lymphadenopathy, and hemophiliacs have had significant exposure rates to HTLV, whereas matched and unmatched control American subjects have rarely been exposed to this agent. In the present experiments, T cells specifically reactive against HTLV were propagated from a patient whose HTLV-bearing lymphoma was in remission. The T cells were cloned in the presence of the virus and an HTLV-specific cytotoxic T-cell clone was isolated. This clone was infected and transformed by the virus, with one copy of an HTLV-I provirus being integrated into the genome. This T-cell clone did not exhibit the normal dependence on T-cell growth factor (interleukin-2) and proliferated spontaneously in vitro. Exposure of the clone to HTLV-bearing, autologous tumor cells specifically inhibited its proliferation and resulted in its death. These results may have implications for HTLV-associated inhibition of T-cell responses.*

The human type-C retrovirus known as human T-cell leukemia-lymphoma virus (HTLV) was first isolated from neoplastic cells derived from black patients in the United States with adult T-cell malignancies (*1, 2*). It has been suggested that HTLV and bovine leukemia virus (BLV) have a common ancestry (*3*).

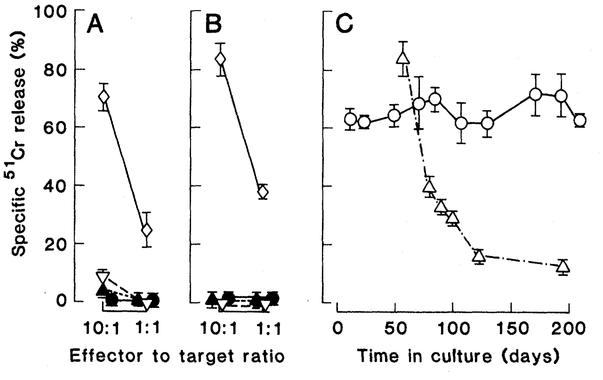

Fig. 1. Functional properties of clone K7. (A) Cytotoxic effector activity of the parent cultured T-cell line (MJ-CTL). (B) Initial cytotoxic effector activity of clone K7 cells derived from MJ-CTL. Standard 4-hour ^{51}Cr-release assays were used to assess the specific cytotoxic activity of cultured T cells as previously described (*15*). The release of radioactivity (*R*) into the surrounding medium by target cells labeled with ^{51}Cr is an index of cell destruction. The percentage specific release of ^{51}Cr was determined by the following formula: $\{[(R_{test}) - (R_s)]/[(R_{max}) - (R_s)]\} \times 100$, where R_{test} is the ^{51}Cr released in the assay, R_s is the spontaneous release, and R_{max} is the maximum release of radioactivity. MJ-CTL and clone K7 cells were tested on day 62 in culture. Target cells were HTLV-bearing autologous tumor cell line, MJ-tumor (◇); HTLV-bearing tumor cell line from an unrelated donor, HUT-102-B2 (▲); Epstein-Barr virus–transformed autologous B cells (●); and an erythroid line, K562 (▽). (C) Progressive loss of cytotoxic activity of clone K7. In each ^{51}Cr release assay, the cytotoxicity of the parent cultured T-cell line, MJ-CTL (○) and clone K7 (△) against autologous HTLV-bearing tumor cells (MJ-tumor cells), was determined. The ratio of effector to target cells for each determination was 10 to 1. Cloning took place on day 35 in culture.