The Storage and Production of Organic Matter in Tropical Forests and Their Role in the Global Carbon Cycle

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ABSTRACT

To investigate the storage relationships between and production of organic matter in tropical forests and climate, data on forest biomass, soil organic matter, litter storage, primary production, and litterfall were surveyed from the literature and organized using the Holdridge Life Zone system of classification. Ordinary least squares regressions were applied to all the data sets using the ratio of temperature to precipitation (T/P) as an index to climate and the independent variable.

Total forest biomass (40-538 t/ha) gave a significant inverted U-shaped relationship with T/P, with peak values in the tropical moist forest life zone and lower ones in wetter and drier forest life zones. Soil carbon content (24-599 t C/ha) decreased exponentially and significantly with increasing T/P (i.e., from wet to dry forest life zones). No significant relationship was found between litter storage and T/P. Gross primary production (19-120 t/ha yr) decreased curvilinearly and significantly with increasing T/P. Neither net primary production (11-21 t/ha yr) nor wood production (1-11 t/ha yr) were related to T/P. The ratio of leaf litter production to net primary production (0.25-0.65) was inversely related to T/P, suggesting different strategies of allocation of the net primary production in different life zones. The relationship between total litterfall (1.0-15.3 t/ha yr, excluding large wood) and T/P was significant and its shape similar to that obtained for biomass versus T/P; litterfall was highest in tropical moist forest life zones and lower in wetter or drier ones. The linear relationship between biomass and litterfall suggested that the turnover time of biomass in mature tropical forests is similar for all life zones, and is of the order of 34 yr.

To determine the role of tropical forests in the global carbon cycle, literature estimates of areas of tropical forests were placed into six life zone groupings. The total tropical and subtropical basal and altitudinal forest area of 1838 million ha was comprised of 42 percent dry forest, 33 percent moist forest, and 25 percent wet and rain forest life zone groups. Organic-matter storage data were also combined into the six life zone groups and the means for each group calculated. The product of forest areas in the six groups and the mean organic matter per unit area in the groups yielded a total storage of 787 billion t organic matter, with vegetation accounting for 58, soils 41, and litter 1 percent. About half of the total storage was located in the tropical basal wet, moist, and dry forest life zone groups. Litterfall data were treated in the same way as organic-matter storage, resulting in a total litter production in tropical forests of 12.3 billion t organic matter/yr. Most litter was produced in the tropical basal moist forest group (30%) and least in the tropical basal dry forest group (10%). Turnover time of litter in tropical forests was less than 1 yr. Lowest turnover times were in very wet (1 yr) and in dry (0.9-1.9 yr) life zone groups.

Tropical forests play an important role in the global carbon cycle because they store 46 percent of the world's living terrestrial carbon pool and 11 percent of the world's soil carbon pool.

UNDERSTANDING HOW THE STORAGE AND PRODUCTION OF ORGANIC MATTER in forests relates to climate is of critical need for management, particularly in tropical latitudes where climatic conditions are more diverse than anywhere else in the world. For example, according to the Holdridge Life Zone system (Holdridge 1967) for classifying plant formations of the world (a system based on mean annual biotemperature and rainfall), the tropical latitudes encompass 66 of the world's 116 life zones and of these, 30 support forests. Holdridge *et al.* (1971) found that the structure of tropical forests varied with life zone, becoming more complex along an increasing humidity gradient, i.e., from arid to perhumid life zones. We hypothesize that storage and production of organic matter in forests also follow a predictable pattern with life zone and believe that knowledge of these relationships will enhance our ability to manage tropical lands. We use the life zone concept as the conceptual framework for our analysis because it has universal applicability, it is based on quantitative climatic relationships using information that is available for many parts of the world, it is an objective method for classifying forest environments, it has been used world-wide (particularly in tropical countries), and it provides the potential for developing predictive equations to fill information gaps for those life zones for which organic-matter storage and/or production information are not available.

Compilations of organic-matter storage and production in tropical forests either consider the "tropics" as being a few ecosystem types (e.g., Whittaker and Likens 1973, Ajtay *et al.* 1979), or they synthesize data for a variety of forest ecosystems without an effort to seek relationships between either production or storage of organic matter and environmental conditions (Murphy 1975, Olson *et al.* 1978, Rodin and Basilevich 1967). Attempts have been made to develop equations to predict net primary productivity at a world level, but these were based on single factors only, such as temperature or rainfall (Lieth 1975). Rosenzweig (1968), however, developed a relationship between net primary production and actual evapotranspiration, but his equation was based mostly on data gathered along a gradient in the Smokey Mountains and does not fit the data base we have for tropical forests.

To begin a rational planning effort for tropical forest lands requires the organization of ecological information, including their organic-matter storage and production potential, because many people either use tropical forests for such products as firewood, food, or fiber, or they convert them to agricultural land or other land uses. Furthermore, these uses can affect the global carbon cycle because tropical forests account for about half of the world's forest areas.

In this paper we review and synthesize available information on the storage and production of organic matter in tropical forests in a usable scheme for both scientists and planners concerned with such issues as global carbon and biomass use. This is one of the products of a three-year study for the U.S. Department of Energy in which we estimated the storage and production of organic matter in tropical forests in order to evaluate their role in the carbon balance of the world. This paper is divided into two parts. First, we summarized what is known about organic-matter storage and production in tropical forests and relate this information to climatic indices for tropical and subtropical life zones. Second, we discuss the role of tropical forests in the carbon balance of the world.

By tropics we mean all those lands with climates that fall within tropical and subtropical life zones of the Holdridge Life Zone system (fig. 1). It is obvious from figure 1 that the data base does not cover

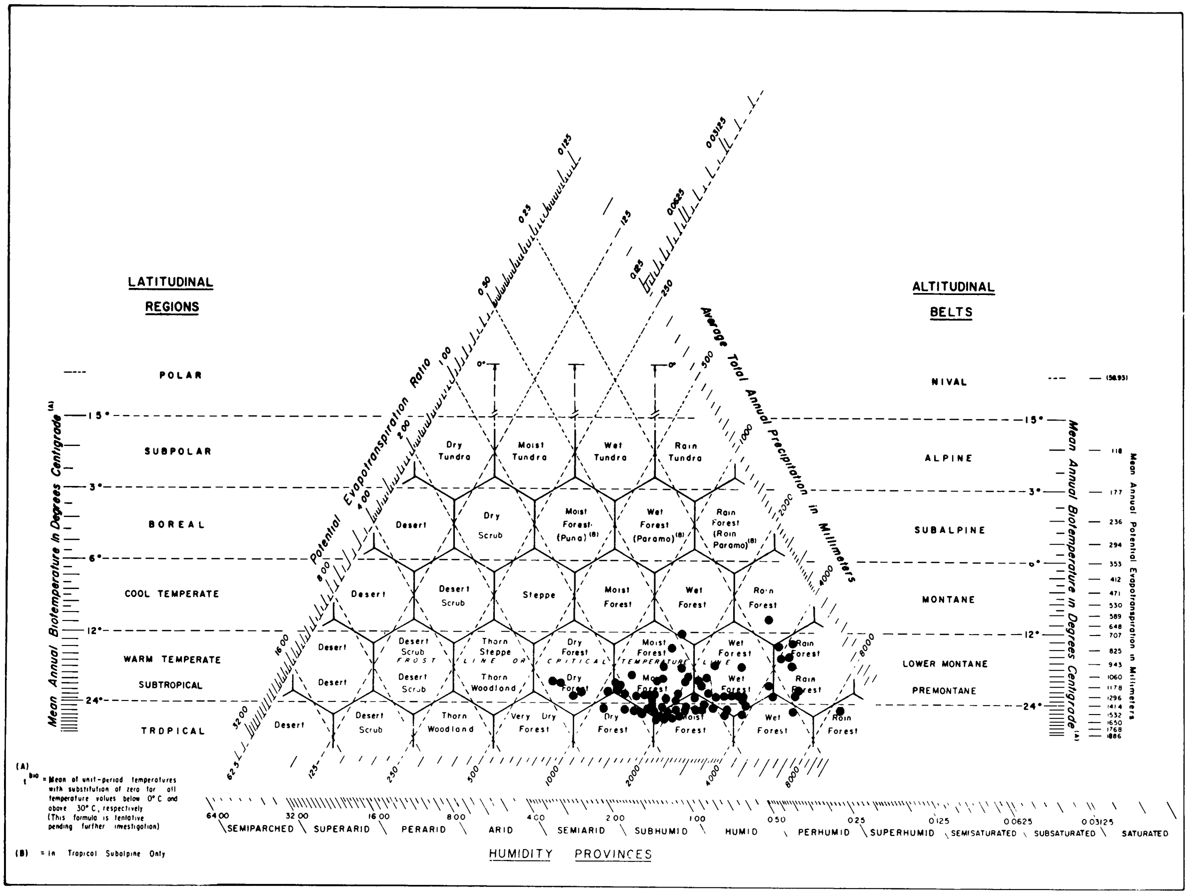

FIGURE 1. Diagram of the Holdridge Life Zone system for classifying world plant formations showing the locations of the study sites used in our analysis.

all life zones of the tropics and subtropics. Instead, the data are heavily concentrated in tropical and subtropical moist life zones with very few studies in very wet or very dry ones.

STORAGE AND PRODUCTION OF ORGANIC MATTER IN TROPICAL AND SUBTROPICAL LIFE ZONES

The amount of organic matter stored or produced in tropical ecosystems was obtained from literature sources. We converted organic carbon units into organic-matter units using a conversion factor of 2g OM/g C. Summarizing information of this type is accompanied by the usual problems of lack of consistency in the reporting of data, papers with incomplete information, inconsistency in methodology, and so on. Data for very young or human-impacted stands and for unique associations with small areal coverage, such as riparian or gallery forests, were omitted from the summary.

Experimental sites were classified into life zones using climatic information given by authors or from the life zone maps. When the information was incomplete we obtained climatic information (long-term where possible) from climatic atlases or other sources. The life zone designation often suggested a different moisture regime than that implied by the author's classification system. For example, the sites in Varanasi, India, were classified as a subtropical moist forest life zone based on long-term climatic data, whereas the authors classified these sites as tropical dry deciduous forest.

To explore relationships between storage and production of organic matter and climate we applied ordinary least square regressions to all the data sets (appendices 1-5) using the ratio of mean annual air temperature (T in °C) to annual precipitation (P in mm/yr) as the independent variable. We used this ratio (T/P) because no assumptions are required to formulate it, and it serves as an index of potential availability of water to plants in the ecosystem (potential evapotranspiration is proportional to air temperature). A more precise index of water availability to plants is the ratio of potential evapotranspiration to precipitation (PET/P). We showed this to be significantly related to the storage of organic matter in tropical forests in our previous analysis (Brown and Lugo 1980), but we did not use it here because its formulation requires knowledge of the biotemperature for each experimental site, and these data are either hard to obtain or require too many assumptions in their calculation. We also did not use actual evapotranspiration because in addition to its unavailability in most tropical areas, it is a measure of the actual amount of water loss as a result of adaptations of vegetation to its environment. For this synthesis we wanted a measure of the environmental conditions to which the plants must adapt in the long-term; the T/P ratio provides such a measure with the least number of assumptions in its formulation.

ORGANIC-MATTER STORAGE.—Total forest biomass exhibited a significant inverted U-shaped relationship with T/P ($p = 0.05$, $r^2 = 0.54$) with peak values in the tropical moist forest life zone (T/P $= 0.7 - 1.4 \times 10^{-2}$) and lower values toward the wetter (T/P $< 0.6 \times 10^{-2}$) or drier life zones (T/P $> 2.0 \times 10^{-2}$) (fig. 2). Although the equation was highly significant and explained more than 50 percent of the variation in the data, it predicted biomass to peak at a lower value and at a lower T/P than the empirical data which peak at about 480 t/ha at a T/P of 1.4×10^{-2}.

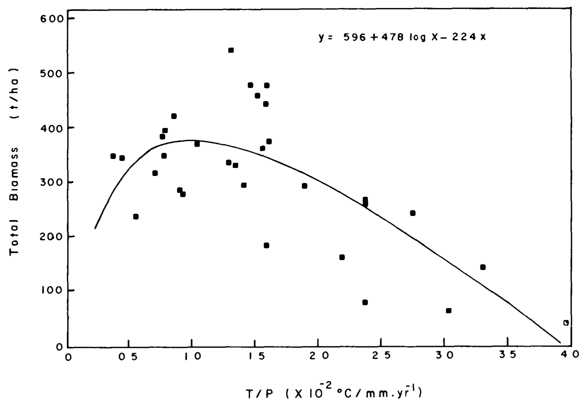

FIGURE 2. Relationship between total biomass and the temperature (T°C) to precipitation (P mm/yr) ratio (significant at $p = 0.05$, $r^2 = 0.54$). When solving the equation, the x value (T/P) must be multiplied by 100.

Soil carbon storage yielded a significant negative exponential relationship ($p = 0.05$) with T/P (fig. 3) but only 23 percent of the variation in the data was explained by the equation. It is clear, however, that both the variability and upper limit in the carbon content of soil decrease with increasing T/P (i.e., towards the drier life zones). Our results are supported by those of Yoda and Kira (1969), who found that the carbon content of soil increased with increasing elevation in Thailand. They found that the soil carbon content doubled (from 57 to 128 t C/ha) over the elevation range 400-1700 m. The increase in elevation implies increasing precipita-

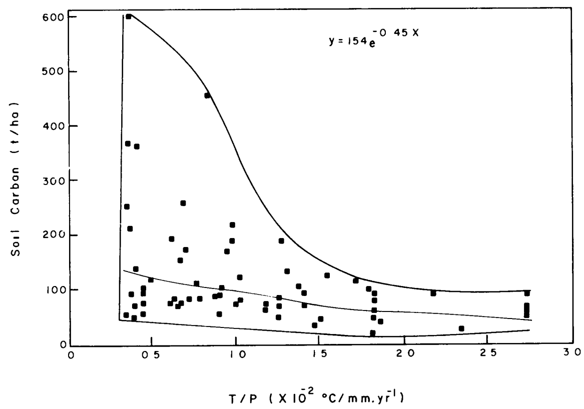

FIGURE 3. Relationship between soil organic carbon content and the temperature (T°C) to precipitation (P mm/yr) ratio (significant at $p = 0.05$, $r^2 = 0.23$). When solving the equation, the x value (T/P) must be multiplied by 100. The statistical line is inside the envelope used to accentuate the range of values.

tion and decreasing temperature and thus decreasing T/P ratio. We found that an exponential function best described their data.

Litter storage was very variable and yielded no significant relationship with T/P.

The relationships presented above suggest that the amount of organic matter stored in plants and, to a lesser degree, in soil in tropical forest ecosystems can be predicted reasonably well from knowledge of precipitation and temperature only. Obviously unique forest associations may not fit these relationships because their structural features may be influenced strongly by edaphic or other atmospheric conditions. However, these relationships are of practical value in determining the long-range effects of changing climate on the earth's biota and its capacity to store organic matter. Significant changes in the earth's climate have been anticipated for the year 2020 as a result of the measured increase in atmospheric CO_2 (Manabe and Wetherald 1975, Wigley *et al.* 1980). If these changes do occur, and shifts in the areal distribution of life zones result, our regression equations could be useful in anticipating the net impact of climate change on organic-matter storage in the tropics.

PRIMARY PRODUCTION.—The primary production data used in this section are summarized in appendix 4, along with the method used by each author. Only five life zones are represented, of which two have more than one citation, and three different methods of measurement were used. The most common method used to estimate primary production was the sum of reproductive parts and leaf litter production and wood production which provides an estimate of only aboveground primary production. Methods of measuring ecosystem production based on changes in biomass over some time period underestimate, and methods based on CO_2 gas exchange closely approximate, the actual energy conversion in plants (Odum 1964). Of the sources cited here, only two used *in situ* measurements of CO_2 gas exchange (Lugo *et al.* 1978, Odum and Jordan 1970) to estimate total plant net primary production, including roots, and gross primary production. Others added respiration rates of plant parts, measured in a laboratory, to net primary production (determined from change in biomass) to estimate gross primary production (Kira 1978, Kira *et al.* 1967, Muller and Nielsen 1965). The estimates of primary production (net and gross) that we give (appendix 4) for the studies of Kira (1978), Kira *et al.* (1967), and Muller and Nielsen (1965) are lower than those given by the authors because we believe that by adding total wood production (minus death of trees) to the sum of leaf, small wood, and large branch litter production (as the original authors did) is double accounting; total wood production includes large branch production, and thus it cannot be added again when it falls as litter. In addition, their method of accounting would make the forest highly productive if for any reason there was a particularly large wood fall. Instead, we used method 2 described in appendix 4. In spite of the paucity of primary production data, some trends do appear:

1. Gross primary production is curvilinearly related to T/P ($p = 0.05$, $r^2 = 0.91$), being high in wet life zones (low T/P) and decreasing toward drier ones (high T/P) (fig. 4).

2. Gross primary production appears to be more sensitive to T/P than other indices of primary production.

3. 74-83 percent of gross primary production was respired by plants in the tropical moist forest life zone compared to 42 percent in the subtropical dry forest.

4. No significant relationship was obtained with total net primary production and T/P, but it is generally higher in moist life zones and decreases slightly towards drier ones (fig. 5).

5. Wood production appears to vary considerably over all life zones (1-11 t/ha yr; fig. 5) with no significant trend. The highest wood production rates were reported for tropical premontane and subtropical moist forest life zones; low rates were reported for a dry forest life zone.

Dawkins (1967) reported total annual wood production values of 4-9 t/ha for what we ascertain to

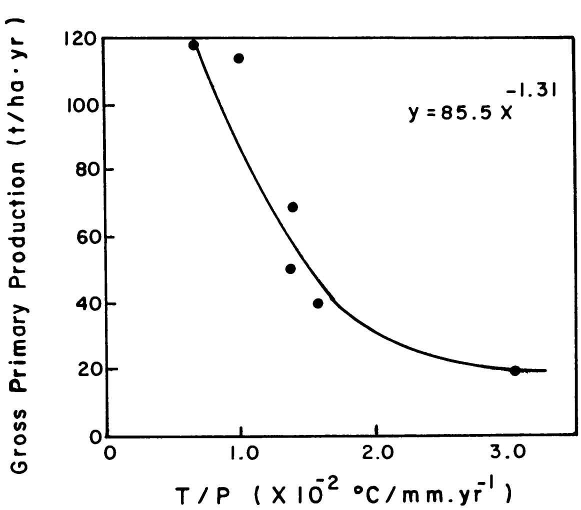

FIGURE 4. Relationship between gross primary production and the temperature (T°C) to precipitation (P mm/yr) ratio (significant at $p = 0.05$, $r^2 = 0.91$). When solving the equation, the x value must be multiplied by 100.

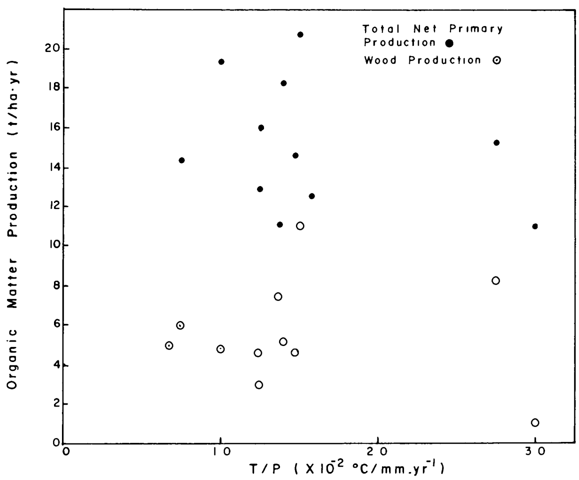

FIGURE 5. Relationships between total net primary production and wood production and the temperature (T°C) to precipitation (P mm/yr) ratio. No significant relationship was obtained with either dependent variable and T/P.

be tropical moist forests and values as high as 27 t/ha for tropical premontane or lower montane wet or rain forests on rich soils. The data we present (appendix 4) suggest a decreasing trend in wood production in wetter life zones which is contrary to Dawkins' (1967) findings. This discrepancy may be due to the differences in soil fertility (Dawkins' values are for rich soils) and/or most likely the data base is too small to make any conclusive statements. The percent of net primary production allocated to wood production did not follow any specific pattern with life zone either (fig. 6). Obviously more net

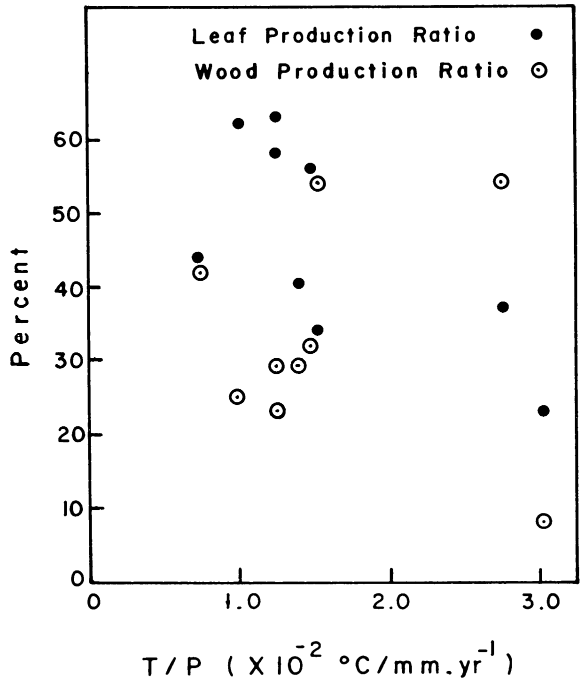

FIGURE 6. Relationships between the ratio of leaf litter production to total net primary production and the ratio of wood production to total net primary production and the temperature (T°C) to precipitation (P mm/yr) ratio. The relationship between the leaf production ratio and T/P ($y = 0.67 - 0.13x$) was significant ($p = 0.05$, $r^2 = 0.50$). When solving the equation, the x value must be multiplied by 100.

primary production and wood production data in all life zones are needed to determine if any significant relationship with climatic factors exists.

Bray and Gorham (1964) suggested that total net primary production of tropical forests could be estimated by multiplying leaf litter production by a factor of 3.3. However, their factor (ratio of total net primary production to leaf litter production) was based on the results from two forests. Our analysis (using the data in appendix 4 and 5 from the same studies) showed that the ratio of leaf litter production to net primary production (the inverse of Bray and Gorham's ratio) was significantly related to T/P ($p = 0.05$, $r^2 = 0.50$; fig. 6). The leaf production ratio was low in drier life zones (higher T/P values) indicating that a small fraction of the forest's net primary production was allocated to leaf litter production; in humid life zones more than 50 percent of net primary production was allocated to leaf litter production. We have shown that Bray and Gorham's proposed factor can vary between 1.5 and 5 depending upon life zone (the inverse of the ratio in fig. 6), and thus estimates of forest net primary production based on leaf litterfall and their factor should be revised.

LITTER PRODUCTION.—The litterfall data and sources used in this section are given in appendix 5. Total litterfall includes leaf, fruit and flowers, twigs, and small branches; it does not include large wood fall. Because rates of litterfall in tropical forests appear to reach steady state values very quickly (Ewel 1976, Kellman 1970), knowing the age of the stand, which often was not given, was not as critical as for organic-matter storage data.

We obtained a significant relationship (at $p = 0.05$, $r^2 = 0.44$) between annual total litter production and T/P (fig. 7). Total litter production is low for very wet life zones ($T/P < 0.6 \times 10^{-2}$) or dry ones ($T/P > 2.5 \times 10^{-2}$) and is highest in the tropical moist forest life zone ($T/P = 1.2 - 1.6 \times 10^{-2}$). Leaf and fruit litter production followed the same trend as for total litter production.

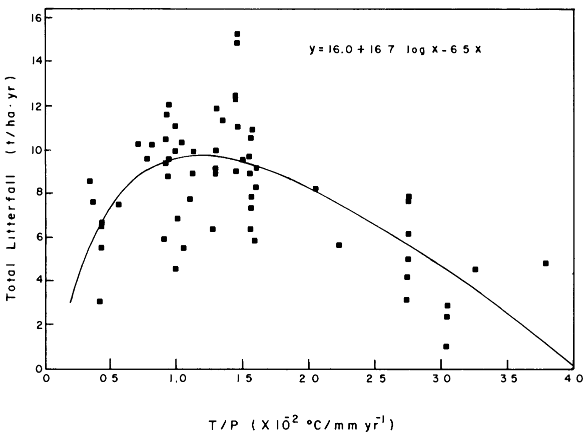

FIGURE 7. Relationship between total litterfall and the temperature (T°C) to precipitation (P mm/yr) ratio (significant at $p = 0.05$, $r^2 = 0.44$). When solving the equation, the x value must be multiplied by 100.

The shape of the litter production versus T/P curve is the same as that obtained for total biomass versus T/P, and as in the biomass curve, predicted peak litter production is lower than observed (9.6 t/ha yr versus > 11 t/ha yr) and occurs at a lower T/P (1.1×10^{-2} versus 1.5×10^{-2}). However, both the predicted and observed peak litter production and total biomass occur in the tropical moist forest life zone. The great similarity between the two curves (litter production and biomass versus T/P) is demonstrated by the significant linear relationship between biomass and litter production ($p = 0.05$, $r^2 = 0.55$, based on biomass and litter production data from the same study only) that we obtained (fig. 8). The slope of the equation has ecological significance because it has units of years and represents turnover time (turnover time = [y - intercept]/x). The significant relationship between biomass and litter production suggests that turnover time of biomass in mature tropical forests is similar for all life zones, and is of the order of 34 yr. But, because large wood fall and root litter production were not included in the litter production measurements (generally they were not measured), turnover time of mature tropical forests is likely to be shorter than 34 yr. However, it could be variable by life zone if net primary productivity turns out to be relatively constant for all climates as implied by the few data in figure 5.

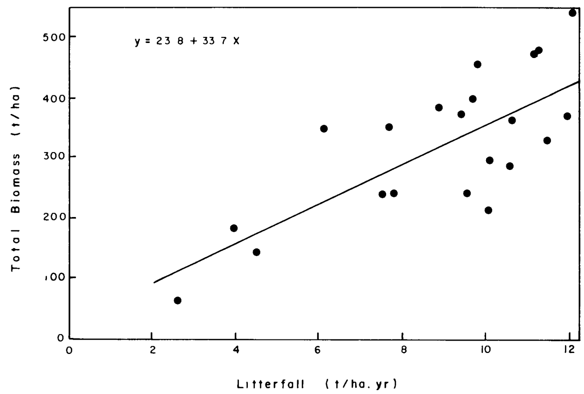

FIGURE 8. Relationship between total biomass and total litterfall (significant at $p = 0.05$, $r^2 = 0.55$).

ORGANIC-MATTER ACCUMULATION THROUGH SUCCESSION BY LIFE ZONE.—To determine if there are general trends in rates of organic-matter (or biomass) accumulation in tropical forests we plotted all aboveground biomass data for different age stands, distinguishing between their differ nt moisture regimes (i.e., dry, moist, wet, or rain forest life zones) but not between tropical or subtropical (fig. 9). Aboveground biomass appears to accumulate very rapidly during the first 10-20 yr, at the end of which biomass in many stands is close to or greater than 100 t/ha. The rate of biomass accumulation appears to be influenced by life zone. Moist forest life zones appear to reach a higher biomass earlier and have a higher biomass at maturity than other life zones. In contrast, dry forest life zones have some of the lowest biomasses in both young and mature stands.

To compare the rates of biomass accumulation in tropical forests with those in temperate forests we produced a graph for temperate forests similar to that shown in figure 9 (fig. 10). Aboveground biomass accumulated fairly linearly in the early years

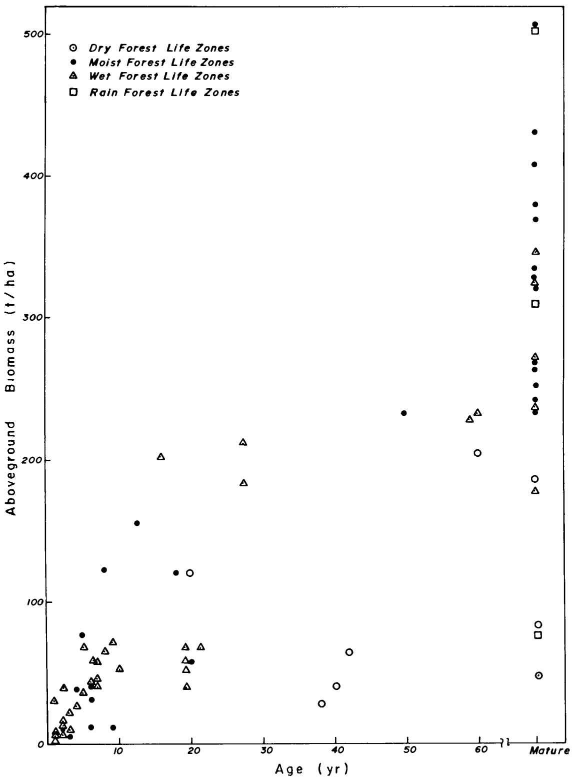

FIGURE 9. Relationship between aboveground biomass in tropical forests and stand age (data are from appendix 1 and the following additional sources: Bartholomew *et al.* 1953. Christensen 1978, Ewel 1971, Lugo *et al.* 1974, Seth and Kaul 1978, Singh 1975, Snedaker 1970).

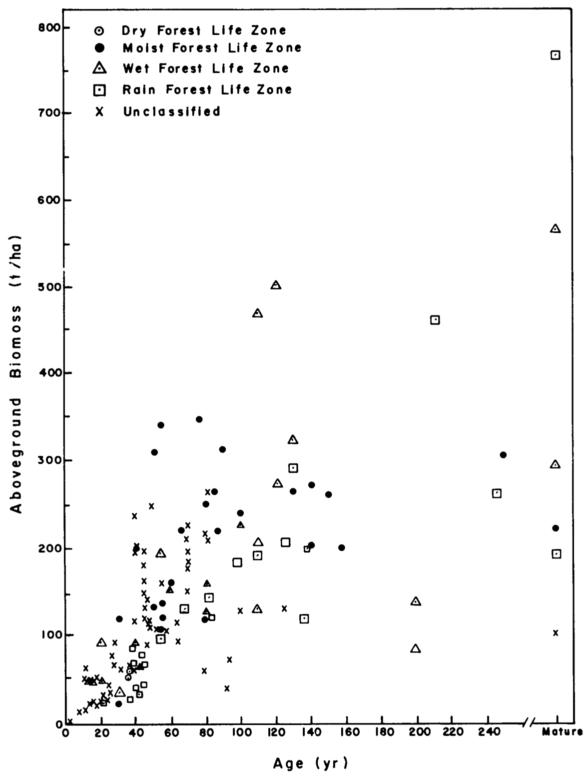

FIGURE 10. Relationship between aboveground biomass in temperate forests and stand age (data are from Art and Marks 1971 [41 stands] and DeAngelis *et al.* 1981 [78 stands]).

(1-40 yr), but it did so at a slower rate than in tropical forests; it took approximately twice as long in temperate forests to reach 100 t/ha than in tropical forests. After age 50 yr temperate forests have a similar range of biomass as tropical forests.

For tropical sites for which time series biomass data were available (which included the following life zones: tropical premontane wet forest, tropical moist forest, tropical moist transition to tropical dry forest, subtropical wet forest, and subtropical moist transition to subtropical dry forest), we observed the following trends:

1. Biomass accumulated quickly in moist and wet forest life zones and about 20 yr were required for total biomass to be as high or almost as high as that of nearby mature forests (Bartholomew *et al.* 1953, Folster *et al.* 1976).

2. Leaf biomass developed rapidly in the early years in all life zones and changed little as the forests matured (Bartholomew *et al.* 1953, Ewel 1971, Folster *et al.* 1976, Snedaker 1970).

3. Litter accumulated quickly in young stands in tropical wet and moist forest life zones and remained fairly constant as the forests matured (Bartholomew *et al.* 1953, Folster *et al.* 1976).

4. Soil organic matter appeared to build up slowly with time in a tropical premontane wet forest (Folster *et al.* 1976).

5. In the early years (first 6 yr only, chosen because all studies gave data to this age) aboveground biomass accumulated fastest in the tropical moist forest (90 t/ha at $T/P = 1.4 \times 10^{-2}$; Bartholomew *et al.* 1953) and at a slower rate in wetter (44-80 t/ha at $T/P = 0.5 - 1.3 \times 10^{-2}$; Ewel 1971, Folster *et al.* 1976, Kellman 1970, Snedaker 1970) and in drier (11.5 t/ha at $T/P = 2.4 \times 10^{-2}$; Drew *et al.* 1978) life zones.

No organic-matter accumulation data were available for tropical or subtropical dry forest life zones. However, Ewel (1977) found that percent cover and leaf area index of successional stands increased at a slower rate in tropical and subtropical dry forest sites than in tropical and subtropical wet forest sites.

Different compartments in a forest reach maximum accumulation of organic matter at different points in time. Ewel (1971) suggested that the leaves accumulate maximum organic matter first, followed by wood and then by roots. This trend was also observed in the data of Bartholomew *et al.* (1953) and of Snedaker (1970). Wood and roots are slower to develop, but they are eventually the compartments that store a large proportion of the organic matter of a forest. Although soil appears to accumulate organic matter at a slow rate (Folster *et al.* 1976), this compartment often stores almost as much organic matter as the sum of the aboveground compartments.

In summary, we found significant relationships between organic-matter storage in vegetation and soils, gross primary production and litter production and climatic factors. Net primary production and wood production appeared not to be related to climatic factors, but this may be due to a paucity of data. Net primary production of all tropical forests cannot be predicted from litterfall using a constant factor because the factor varies with climate. The turnover time of plant organic matter appears to be similar for all tropical forests regardless of life zone. Biomass accumulates faster in tropical moist forest life zones than in wetter or drier ones and faster than in temperate forests during the early stages of succession.

THE ROLE OF TROPICAL FORESTS IN THE GLOBAL ORGANIC CARBON CYCLE

The role of tropical forests in the global organic carbon cycle is dependent upon the area of tropical forests, the amount of organic carbon (as organic matter) stored in them, and the rate at which organic carbon is fixed by plants and exchanged with other ecosystems. The exchange of organic carbon between forests and other ecosystems through runoff and river is not discussed in this paper, and readers are referred to Brown and Lugo (1981) and Likens *et al.* (1981). Because we found that the storage and production of organic matter in tropical forests correlates significantly with life zone, any analysis of the role of tropical forests in the global organic carbon cycle must include a classification of world forests by life zone and a calculation of their organic carbon storage and turnover based on values typical for each category. This is the analysis that we perform below.

AREAS OF TROPICAL LANDS AND FORESTS.—We evaluated several sources which gave estimates of tropical forest areas (Lanly and Clement 1979; Myers 1980; Persson 1974, 1975, 1977; Sommer 1976; UNESCO 1978), but for our analysis we used the land and forest areas given by Persson, because, in our opinion, he used the most reliable and thorough approach. The year of Persson's appraisal varied by country, and he suggested that the estimates were for the early 1970's, probably 1972-73. His detailed country notes also facilitated the placement of tropical forests into life zones (see next section). We did not use the more recent appraisal of tropical forest areas (for 1975) by Lanly and Clement (1979) because it was not detailed by country, which is necessary for our analysis. Nor did we use the recent assessment of tropical forest areas by Myers (1980) because he included only half the countries that have tropical forests.

Using our definition of the "tropics" (see introduction), they encompass an area of $48{,}443 \times 10^3 km^2$

TABLE 1. *Areas of tropical lands and forests.*[a]

Region	Land area	Total forest area	Area closed forest[b]	Area open woodland[c]	Closed forest to land area	Open forest to land area
	($10^3 km^2$)				(%)	
Africa	22,659	8246	1904	6342	8	28
Asia	6846	2665	2515	151	37	2
Central America	1746	585	557	28	32	2
South America	14,106	5988	5058	930	36	7
Oceania	3086	896	405	491	13	16
Total	48,443	18,380	10,439	7942	22	16

[a]From Persson (1974, 1975, 1977).

[b]Closed forest=land with trees whose crowns cover more than 20 percent of the area and used primarily for forestry purposes, giving mainly industrial wood (Persson 1974).

[c]Open woodland=land with trees whose crowns cover 5-20 percent of the area and used primarily for forestry purposes, producing a substantial supply of wood, at least fuelwood and poles for local consumption. Some open woodlands may be covered with trees whose crowns cover more than 20 percent of the area, but do not supply industrial wood.

of which 38 percent is forested as of the early 1970's (table 1). Closed forests account for 58 percent of the total forest area and open woodlands for the remaining 42 percent. Africa has the largest area of open woodland and Asia and Central America the least. Approximately 50 percent of the tropical closed forests are located in South America.

Our estimate of total tropical forest area (18,380 $\times 10^3 km^2$) is 83 and 75 percent of the respective estimates used by Olson *et al.* (1978) and by Whittaker and Likens (1973) and 124 percent of that used by Ajtay *et al.* (1979) in their estimates of storage and production of organic matter in tropical forests.

LIFE ZONE DISTRIBUTION OF TROPICAL LANDS AND FORESTS.—To estimate the storage and production of organic matter in the total tropical region we need to know the area of forest land in a particular forested life zone (of which there are 30). This information is not currently available. However, by combining life zones into larger groups based on both the humidity provinces (fig. 1) and altitude, we eliminated the need for detailed information, yet maintained the conceptual strength of the life zone system. Life zones were combined into six groups, representing gradients from wet to dry and lowlands to highlands, as follows (fig. 1): 1) tropical basal (TB) wet and rain forest—includes tropical wet forest and tropical rain forest; 2) tropical basal (TB) moist forest—includes tropical moist forest; 3) tropical basal (TB) dry forest—includes tropical thorn woodland, very dry forest, and dry forest; 4) subtropical and tropical (S and T) wet and rain forest—includes subtropical (basal) wet forest and rain forest, tropical premontane wet forest and rain forest, tropical and subtropical lower montane and montane wet forest and rain forest; 5) subtropical and tropical (S and T) moist forest—includes subtropical (basal) moist forest, tropical premontane moist forest, tropical and subtropical lower montane and montane moist forest; 6) subtropical and tropical (S and T) dry forest—includes subtropical (basal) thorn woodland and dry forest, tropical premontane thorn woodland and dry forest, tropical and subtropical lower montane dry forest.

The lands of each tropical country were then placed into these six life zone groupings by one of the following two procedures. For those countries for which life zone maps were available the areas of the life zone groupings were obtained directly from the maps or accompanying reports. Maps and/or reports were available for the following countries: Australia (Holdridge, unpubl. map), Bolivia (Unsueta *et al.* 1975), Colombia (Espinal and Montenegro 1963), Costa Rica (Tosi 1969), Dominican Republic (Tasaico 1967), Ecuador (Gortaire Iturralde *et al.* 1963), El Salvador (Holdridge 1977), Guatemala (Holdridge *et al.* 1978), Honduras (Holdridge 1962), Mozambique (Soares and Barreto 1972), Nicaragua (Agencia para el Desarrollo Internacional del Gobierno de los Estados Unidos de America 1962), Nigeria (Tosi 1968), Panama (Food and Agriculture Organization 1971), Paraguay (Food and Agriculture Organization 1969), Peru (Tosi 1981), Puerto Rico (Ewel and Whitmore 1973), Thailand (Holdridge *et al.* 1971), and Venezuela (Ewel and Madriz 1968). For the remaining countries, the percent of each of the six life zone groupings within a given country was established from vegetation, climate, and topographic maps (J. Tosi and L. Holdridge, pers. comm.) and multiplied by the area of the country to obtain the area of the life zone group.

We used Persson's (1974, 1975, 1977) forest inventory and country notes and the distribution of the life zone groups within a country to assign forest areas to the life zone groups. In general, Persson's open forest category was assigned to S and T and, in some cases, to TB dry forest life zone groups. The closed forest category was assigned to the other life zone groups in proportion to the distribution of the life zone groups within a country and/or by matching Persson's country notes.

The results of this analysis (table 2) show that 46 percent of tropical lands is occupied by TB and S and T dry forest life zone groups, 38 percent by TB and S and T moist forest life zone groups, and only 16 percent by TB and S and T wet and rain forest life zone groups. Most of the dry forest life zone groups are in Africa (67%) and the least in Central and South America (< 10%). Central and South America (combined) has the largest land area of the very wet life zone groups (45% in TB and S and T wet and rain forest), with the remainder approximately equally distributed between Africa and Asia (25% each).

The total tropical forest area is comprised of 42 percent TB and S and T dry forest life zone groups, 33 percent TB and S and T moist forest life zone groups, and 25 percent TB and S and T wet and rain forest life zone groups (table 2). Tropical basal (lowland) life zone groups account for 40 percent of the total tropical forest area. A larger proportion of the land area is forested in the very wet life zone groups (potential evapotranspiration ratio < 0.5, cf. fig. 1). For example, 93 percent of the land area in TB and S and T wet and rain forest life zone groups is forested in Central and South America combined, 55 percent is forested in Africa, and 51 percent is

TABLE 2. *Distribution of tropical lands[a] and forest areas[b] into the six life zone groupings by continent. (Numbers are in 10^6 ha, with percentages in parentheses.)*

Life zone grouping[c]	Africa		Asia		Central America		South America		Oceania		Total	
	Forest	Land	Forest	Land	Forest	Land	Forest	Land	Forest	Land	Forest	Land
TB-wet and rain forest:	76.2(9)	136.3(8)	2.6(1)	5.9(1)	4.0(7)	5.1(3)	126.9(21)	128.3(10)	—	—	209.7(11)	275.6(7)
TB-moist forest:	89.9(11)	184.2(11)	76.2(29)	159.8(23)	2.4(4)	7.0(4)	166.8(28)	430.5(35)	11.3(13)	14.4(5)	347.0(19)	795.9(19)
TB-dry forest:	85.5(10)	177.0(10)	8.4(3)	19.1(3)	0.1 —	1.3(1)	79.5(13)	209.9(17)	4.0(4)	4.6(2)	177.5(10)	411.9(10)
S and T-wet and rain forest:	15.2(2)	28.7(2)	79.3(30)	155.5(23)	17.0(29)	21.0(12)	118.8(20)	133.5(11)	25.5(28)	27.7(10)	255.8(14)	366.4(9)
S and T-moist forest:	93.6(11)	217.2(12)	73.9(28)	226.9(33)	16.1(28)	55.7(33)	72.0(12)	257.3(21)	4.1(5)	29.2(10)	259.7(14)	786.3(19)
S and T-dry forest:	464.4(56)	992.4(57)	25.8(10)	117.6(17)	18.9(32)	80.4(47)	34.8(6)	72.5(6)	44.7(50)	212.2(74)	588.6(32)	1475.1(36)
Totals:	824.8	1735.9	266.6	684.8	58.5	169.5	598.8	1232.0	89.6	288.1	1838.3	4111.2[d]

[a]Lands that fall within the subtropical and tropical life zones.

[b]Includes open and closed forest area from table 1.

[c]TB = tropical basal (lowland), S and T = subtropical basal and other subtropical and tropical altitudinal belts.

[d]This is less than the total land area given in table 1 because it does not include non-forested life zones (cf. fig. 1).

forested in Asia. In contrast, in the life zone groups with potential evapotranspiration ratio of 0.5-1.0 (TB and S and T moist forest) a smaller proportion of the land is forested (35-45% of the land area in Central and South America, Africa, and Asia). The moist forest life zones generally support the highest intensity of human activity and are those that succumb quicker to deforestation (Tosi and Voertman 1964).

TOTAL ORGANIC-MATTER STORAGE IN TROPICAL FORESTS.—To estimate the storage of organic matter in all tropical forests we first combined the organic-matter storage data (appendices 1-3) into the six life zone groupings and calculated the mean of each compartment of each of the groups. We used the appropriate regression equations (figs. 2 and 3) to estimate organic-matter values for those life zone groups which had one or no value using an average T/P for that life zone group. Grouping the data this way shows that the TB wet, moist, and dry forest life zone groups store more organic matter per unit area than do those in the corresponding S and T life zone groups (table 3). More organic matter is stored in vegetation than in soil in all life zone groups except the S and T wet and rain forest in which storage in vegetation is similar to that in soil. Organic matter stored in litter accounts for a small fraction only of the total (0.5-3.5%).

The relationships between mean organic matter in vegetation and in soils in the six life zone groups (variances were homogeneous at $p = 0.05$) versus their T/P (calculated as the mean of the individual points used in the groupings) were significant ($p = 0.05$, $r^2 = 0.98$ and 0.83 for vegetation and soil, respectively) and of similar shape to those obtained from the individual points (compare figs. 2 and 3 with fig. 11). No significant relationship was obtained for litter in the life zone groups. This similarity in the shape of the curves, obtained whether the data are grouped or not, gives us confidence in the way we combined life zones. Total organic matter (sum of vegetation, soil, and litter) in the six life zone groups was linearly related to T/P (significant at $p = 0.05$, $r^2 = 0.90$; fig. 11). In wetter life zone groups ($T/P < 1.0 \times 10^{-2}$) the lower organic matter in vegetation is compensated for by the high soil organic matter.

Finally, we multiplied the area of tropical forests in the six life zone groups (table 2) by the organic matter stored per unit in the groups (table 3) to obtain our best estimate of the total storage of organic matter in tropical forests (table 4). Of the total amount stored (787 billion tons), vegetation ac-

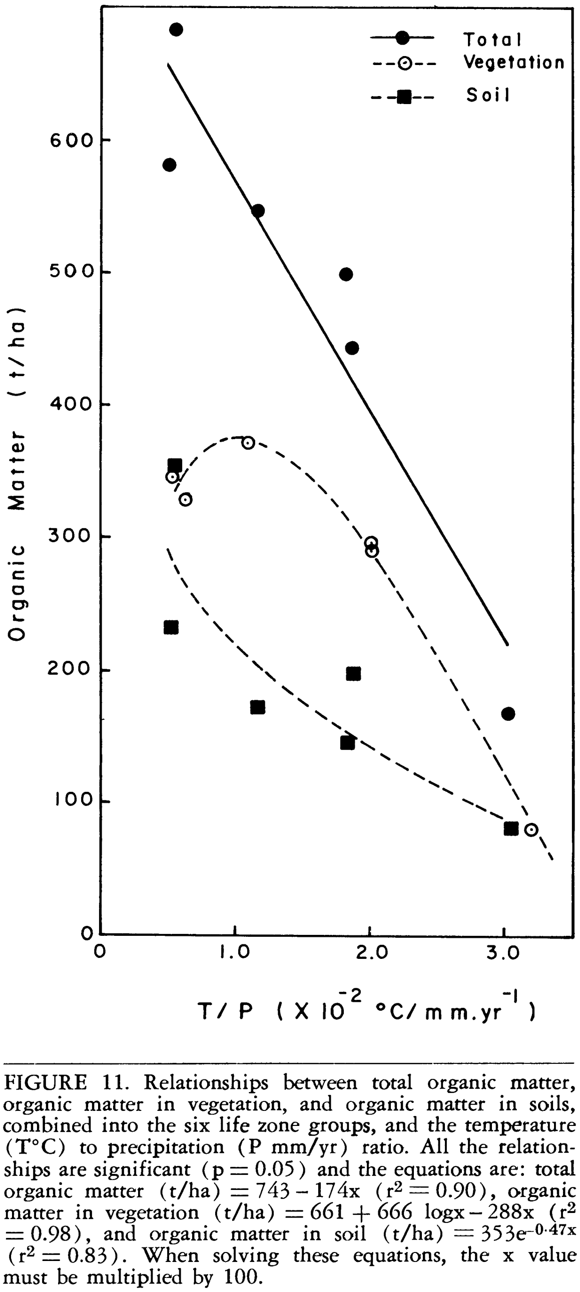

FIGURE 11. Relationships between total organic matter, organic matter in vegetation, and organic matter in soils, combined into the six life zone groups, and the temperature (T°C) to precipitation (P mm/yr) ratio. All the relationships are significant ($p = 0.05$) and the equations are: total organic matter (t/ha) $= 743 - 174x$ ($r^2 = 0.90$), organic matter in vegetation (t/ha) $= 661 + 666 \log x - 288x$ ($r^2 = 0.98$), and organic matter in soil (t/ha) $= 353e^{-0.47x}$ ($r^2 = 0.83$). When solving these equations, the x value must be multiplied by 100.

counts for 58 percent, soils 41 percent, and litter 1 percent. About half (49%) is stored in the TB life zone groups whereas these life zone groups account for 40 percent of the forested area. The two dry forest groups account for 22 percent of the total organic matter in tropical forests, yet they cover the largest forested area (42%). The TB moist forest life zone group stores more organic matter (24%) than any of the other five groups.

Our final estimate of the total organic matter in tropical forests is influenced by three major factors: the area of forests, the organic matter stored per unit area in a life zone group, and the T/P value chosen to represent a life zone. If the forest area is reduced by 10 percent, equally distributed in all life zone groups, we get a corresponding reduction in the total storage of organic matter in tropical forests. But, if it is reduced by 10 percent in the TB moist forest life zone group only, we get a 13 percent reduction in the total (table 5). A 10 percent decrease in the mean T/P used to represent a life zone group (i.e., the life zone groups were more humid than indicated by the data base) produced the least change in our estimate. In general, our estimate appears not to be very sensitive to any one of the factors taken individually (table 5). And, even in combination, the positive effects could compensate for the negative ones.

LITTER PRODUCTION IN TROPICAL FORESTS.—Because data on gross and net primary production of tropical forests are limited (appendix 4) and the values of net primary production were unrelated to T/P, we feel that we cannot make a meaningful estimate of the primary production of organic matter in tropical forests at this time. However, litter production data are more abundant, and we did obtain a significant relationship with T/P.

We treated the litter production data in the same way as organic-matter storage data to produce table 6. Forests in the TB life zone groups produce more litter than in the corresponding S and T group. However, the difference in production between the two wet and rain forest life zone groups is not significant. Leaf and fruit litter production is 69 to 86 percent of the total. The significant relationship between total litter production and T/P for the six life zone groups ($p = 0.05$, $r^2 = 0.87$, fig. 12) and its similarity in shape to that obtained from the individual points (cf. fig 7) is further support for our choice of life zone groupings.

Total production of litter in tropical forests is 12.3 billion t/yr (the product of forest area [table 2] and litter production [table 6] by life zone group) of which 53 percent is produced in the three TB life zone groups (table 7). Most litter is produced in the TB moist forest group (30%) and least in the TB dry forest group (10%).

The turnover time of litter in tropical forests is less than 1 yr (table 7). Turnover times are shorter in the TB life zone groups (0.57-0.88 yr) than in the S and T groups (0.70-1.86 yr). Litter turns over fastest in the two moist forest groups and slowest in the two dry forest groups.

TABLE 3. *Organic-matter storage in life zone groups. One standard error is given in parentheses.*

Life zone grouping[a]	n	Organic matter: Vegetation (t/ha)	n	Soil[b] (t/ha)	n	Litter (t/ha)	Total (t/ha)
TB-wet and rain forest	—	344 (31)[c]	9	230 (64)	—	6.0 (0.5)[d]	580
TB-moist forest	14	369 (27)	15	170 (12)	13	6.1 (0.6)	545
TB-dry forest	—	292 (21)[c]	7	142 (24)	—	6.0 (0.5)[d]	440
S and T-wet and rain forest	8	322 (20)	22	350 (60)	7	7.6 (1.6)	680
S and T-moist forest	10	291 (29)	15	196 (32)	9	5.2 (0.9)	492
S and T-dry forest	4	80 (22)	—	78 (21)[c]	4	5.8 (1.3)	164

[a]TB = tropical basal (lowland), S and T = subtropical basal and higher elevations plus tropical premontane and other tropical higher elevation life zones.

[b]Assumed organic-matter content = 2.0 × organic carbon.

[c]Mean and standard error estimated from regression of total biomass or soil organic matter and T/P using average conditions for life zone: for TB-wet and rain forest $T = 26°C$, $P = 5000$ mm/yr $(T/P = 0.52 \times 10^{-2})$, for TB-dry forest $T = 27.5°C$, $P = 1350$ mm/yr $(T/P = 2.0 \times 10^{-2})$, for S and T-dry forest $T = 25°C$, $P = 825$ mm/yr $(T/P = 3.03 \times 10^{-2})$.

[d]Mean and standard error of litter storage values in all life zones.

TABLE 4. *Organic-matter storage in tropical forests. (One standard error is given in parentheses.)*

Life zone grouping[a]	Area (10^6ha)	Vegetation (10^9t)		Soil (10^9t)		Total storage[b] (10^9t)	(%)
TB-wet and rain forest	209.7	72.1	(6.5)	48.2	(13.4)	121.6	15
TB-moist forest	347.0	128.0	(9.4)	59.0	(4.2)	189.1	24
TB-dry forest	177.5	51.8	(3.7)	25.2	(4.3)	78.1	10
S and T-wet and rain forest	255.8	82.4	(5.1)	89.5	(15.4)	173.9	22
S and T-moist forest	259.7	75.6	(7.5)	50.9	(8.3)	127.8	16
S and T-dry forest	588.6	47.1	(13.0)	45.9	(12.4)	96.5	12
Total:	1838.3	457.0	(45.2)	318.7	(58.0)	787.0	

[a]TB = tropical basal (lowland), S and T = subtropical basal and higher elevation life zones and all tropical altitudinal life zones.

[b]Total storage includes litter.

TABLE 5. *Sensitivity of total organic matter in tropical forests to changes in forest area, in organic matter stored per unit area, and in T/P.*

Changes	Total organic matter (10^9t)	% change in baseline[a]
10% reduction in forest area in each life zone group	708	−10
10% reduction in forest area, all in TB-moist forest group	686	−13
± 1 S.E. in vegetation and in soil	892 682	±13
10% decrease in mean T/P for each life zone group[b]	857	+9
20% decrease in mean T/P for each life zone group[b]	914	+16
10% increase in mean T/P for each life zone group[b]	733	−7
20% increase in mean T/P for each life zone group[b]	688	−12

[a]Baseline = 787 × 10^9t (table 4).

[b]Each new T/P resulting from the change was substituted into the regression equation of total organic matter versus T/P (fig. 11) to obtain a new estimate of organic-matter storage per unit area.

TABLE 6. *Litter production in the six life zone groups. (One standard error is given in parentheses.)*

Life zone group[a]	n[b]	Litter production (t/ha yr): Leaves and fruit	Total
TB-wet and rain forest	—	—	7.90 (0.50)[c]
TB-moist forest	16/21	7.46 (0.32)	10.62 (0.49)
TB-dry forest	—/2	—	6.9 (1.3)
S and T-wet and rain forest	10/14	5.42 (0.52)	7.83 (0.66)
S and T-moist forest	13/21	6.43 (0.49)	7.41 (0.40)
S and T-dry forest	5/5	2.37 (0.51)	3.12 (0.70)

[a]TB = tropical basal (lowland), S and T = subtropical basal and higher elevation life zones and all tropical altitudinal life zones.

[b]Two numbers give the sample size for leaves and fruit and total litter production, respectively.

[c]From regression of total litterfall versus T/P (fig. 7) using $T = 26°C$ and $P = 5000$ mm/yr $(T/P = 0.52 \times 10^{-2})$.

TABLE 7. *Litter production, standing crop, and turnover time in tropical forests. (One standard error is given in parentheses.)*

Life zone grouping[a]	Total litter production (10^9t/yr)	Litter storage (10^9t)	Turnover time (yr)
TB-wet and rain forest	1.66 (0.10)	1.26 (0.10)	0.76
TB-moist forest	3.69 (0.17)	2.12 (0.20)	0.57
TB-dry forest	1.22 (0.24)	1.07 (0.08)	0.88
S and T-wet and rain forest	2.00 (0.17)	1.95 (0.40)	0.97
S and T-moist forest	1.92 (0.11)	1.35 (0.23)	0.70
S and T-dry forest	1.84 (0.41)	3.41 (0.77)	1.86
Total	12.33 (1.20)	11.16 (1.78)	0.91

[a]TB = tropical basal (lowland), S and T = subtropical basal and higher elevation life zones plus all tropical altitudinal life zones.

Total production and storage of litter are sensitive to the same factors as are our organic-matter storage estimates. Changes in any one of the three factors produced a less than 15 percent change in litter production or litter storage estimates, a response similar to that of total organic-matter storage.

COMPARISON OF STORAGES AND PRODUCTION OF ORGANIC CARBON IN THE TROPICS.—Our final estimate of organic-matter storage (converted to organic carbon to facilitate comparisons) in tropical forests contrasts sharply with other estimates (tables 8 and 9). The estimate of organic matter in vegetation obtained by Whittaker and Likens (1973) is double our estimate, and those of Ajtay *et al.* (1979) and Olson *et al.* (1978) are only slightly higher than ours. Olson *et al.'s* and Schlesinger's (1980) estimates for organic carbon stored in soils are about double our estimate, whereas Ajtay *et al.*'s estimate is slightly lower than ours. The differences between our estimate and those of others are most likely due to: 1. Differences in definition of the tropics. 2. Differences in estimates of the area of tropical forests—Whittaker and Likens and Olson *et al.* used higher estimates and Ajtay *et al.* used lower estimates than ours. The high estimate of Whittaker and Likens is reportedly for the 1950's, whereas the lower estimate of Ajtay *et al.* (based somewhat on Whittaker and Liken's area estimate) is for the present. The differ-

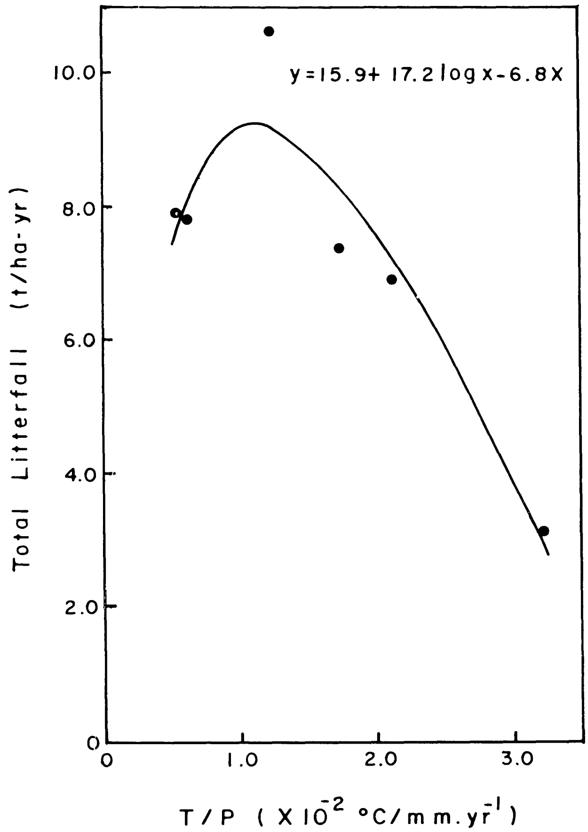

FIGURE 12. Relationship between total litterfall combined into the six life zone groups and the temperature (T°C) to precipitation (P mm/yr) ratio (significant at $p = 0.05$, $r^2 = 0.87$). When solving the equation, the x value must be multiplied by 100.

TABLE 8. *Estimates of organic-carbon[a] storage in vegetation in tropical forest ecosystems.*

Source	For year:	No. of forest categories	Area of forests (10^6ha)	Range of organic-carbon storage in forests (t C/ha)	Total organic-carbon storage in vegetation (10^9t C)
This study	early 1970's	6	1838	46-183	228
Ajtay *et al.* 1979	1970's	3	1480	113-189	244
Olson *et al.* 1978	1970	6	2220	70-180	254
Rodin *et al.* 1975	b	3	5535	54-220	674
Whittaker and Likens 1973	1950	2	2450	160-200	460

[a]Assumed C = 50% × organic matter.

[b]Assumed that vegetation existed in its precultivated or natural state.

TABLE 9. *Estimates of organic-carbon storage in soil in tropical forest ecosystems.*

Source	Area (10^6ha)	Storage of soil organic carbon (10^9t C)
This study	1838	159
Ajtay *et al.* 1979	1480	123
Olson *et al.* 1978	2220	307
Schlesinger 1980	2450	288

ence between these two estimates was suggested to be a result of deforestation of tropical forests (Ajtay *et al.* 1979). This difference of 970 million ha represents about 1.6 percent deforestation/yr for the whole tropics. However, recent estimates of deforestation give 0.4-0.6%/yr (Seiler and Crutzen 1980), 0.7%/yr (Lugo and Brown 1981) and 0.5%/yr (Lanly and Clement 1979) with values as high as 1.3%/yr in such high population density areas as parts of Venezuela (Hamilton 1976), and 3%/yr in industrializing countries such as Costa Rica (Tosi 1980). Because recent estimates of deforestation are lower than the values implied in the area estimate of Ajtay *et al.*, we conclude that either they have underestimated the area of tropical forests and/or that Whittaker and Likans overestimated the area in the 1950's. 3. Differences in the conversion factor from organic matter to carbon—Ajtay *et al.* used a conversion factor of 0.45 and we used a factor of 0.50. Using the carbon content values in Ajtay *et al.* (their table 5.4) we calculated an average carbon content in forest living components and forest ecosystem to be 0.51, closer to our value. 4. Conceptual differences—with the exception of Olson *et al.* the other estimates ignored the variability in tropical environments by dividing tropical forests into two or three categories.

Our estimate of litter production in tropical forests also differs from estimates made by others. Ajtay *et al.* (1979) estimated litter production in the tropics to be 11.0 billion t C/yr and Reiners (1973) estimated a value of 11.4 billion t C/yr. Both of these estimates are about double that of ours of 6.2 billion t C/yr (table 7, carbon = 0.5 organic matter). The main reason for this discrepancy is that Ajtay *et al.* and Reiners used average annual litter production rates that were about 2.0 times and 1.7 times higher, respectively, than the average annual litter production rate we used. In addition, Ajtay *et al.* used a lower forest area (1480 million ha) and Reiners a higher forest area (2000 million ha) than we used.

The most controversial of the data used in any of the estimates is the area of tropical forests. However, as new and better estimates of the areas of tropical forests become available, our approach will enable these new estimates to be used in conjunction with the regression equations of organic-matter storage and production versus T/P (figs. 10 and 11) to revise the global numbers.

COMPARISON WITH OTHER BIOMES.—We have estimated that the world's biota stores 500 billion metric tons (BMT) of carbon and that the soils of the world store an additional 1380 BMT (Brown and Lugo 1981). Tropical forests, accounting for about half of the world's forest area, store 46 percent of the world's living terrestrial carbon pool. No other biome stores as much carbon in the biota. However, tropical forests store only 11 percent of the world's soil carbon pool. Boreal forests, tundra, grasslands, and peatlands store more carbon in the soil than do tropical forests.

The export of organic carbon from tropical forest lands was higher on a unit area basis than from any other biome (11.3 g C/m^2 yr vs a range of 0.62-6.12 g C/m^2 yr for all biomes including temperate wetlands; Brown and Lugo 1981). Total export of organic carbon to the ocean was reported to be a conservative 0.2 BMT C/yr, or an export that is much higher than that of any other biome.

It appears then that tropical forests play a major role in the global cycle of organic carbon by: storing approximately 20 percent of the world's terrestrial carbon pool (including vegetation and soil); exhibiting a rapid turnover rate of organic carbon (reflected in the fast litter turnover and fast accumulation of organic matter during succession), and, therefore, representing a carbon reservoir that is very responsive to any perturbation; and exporting large quantities of organic carbon to the ocean and thus acting as a constant sink of atmospheric carbon.

In summary, our synthesis has shown that organic-matter storage and production in tropical forests are related to climatic factors. We have also demonstrated that significant information gaps exist, particularly for forests growing at the environmental extreme of the tropics. Given the importance of the tropical biome to the earth's organic carbon cycle, it behooves us to support ecosystem level research in order to improve our ability to use and manage these poorly understood ecosystems.

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APPENDIX 1. *Organic-matter storage in vegetation.*

Life zone[a]	T[b] (C°)	P[b] (mm/yr)	Age (yr)	Organic matter (t/ha) Above	Below[c]	Total	Source
T-lower montane rain forest	13	4000	Mature	310	39	349[d]	Edwards and Grubb 1977
T-wet forest	27	3726	Mature	322	60	382	Hozumi *et al.* 1969
T-premontane wet forest	20	2300	Mature	271	13	284	Golley *et al.* 1975
	22	4200	27	197	39[e]	236	Kellman 1970
T-montane wet forest	12	1500	Virgin	347	73	420	Brun 1976
T-moist forest	25.5	1807	Mature	432	42	474	Bandhu *et al.* 1973, Kira 1978
	26.2	3521	Mature	340	56	396	Brunig *et al.* 1979, Jordan and Uhl 1978, Stark and Spratt 1977
	27	3000	Virgin	326	55[f]	381	Folster *et al.* 1976
	27	3000	Virgin	179	30[f]	209	Folster *et al.* 1976
	27	3000	16	203	34[f]	237	Folster *et al.* 1976
	26	2000	Mature	316	11	327	Golley *et al.* 1975
	26.2	2100	Mature	513	25	538	Huttel and Bernhard-Reversat 1975, Huttel 1975
	27.2	1771	Mature	309	132	441	Klinge cited in Jordan and Uhl 1978
	26.2	3521	Mature	377	104	481	Klinge and Herrera 1978
	26.2	3521	Mature	192	97	289	Klinge and Herrera 1978
	26.2	3521	Mature	147	120	267	Klinge and Herrera 1978
	26	1900	Virgin	243	48	291	Muller and Nielsen 1965
	27	2700	Mature	334	32	366	Ogawa *et al.* 1965
	27.2	1771	Mature	406	67	473	Klinge cited in Edwards and Grubb 1977, Fittkau and Klinge 1973
T-premontane moist forest	20	1270	?	146	35	180	Bandhu *et al.* 1973
	20	1600	?	286	46[g]	332	Enright 1979
	20	1270	Mature	320	51[g]	371	Freson *et al.* 1974
	25	1651	50	305	54	359	Greenland and Kowal 1960
	26.5	1800	Mature	431	24	455	Huttel and Bernhard-Reversat 1975, Huttel 1975
S-lower montane wet forest	15	3000	Mature	279	65	344[h]	Tanner 1980a
S-wet forest	23	3450	Mature	237	116	353	Crow 1980
	23	3450	Mature	228	89	317	Jordan 1971
	23	3450	Mature	198	73	271	Odum 1970, Ovington and Olson 1970
S-moist forest	30	1100	60	205	34	239	Bandhu 1973
	27	1147	Mature	253	10	263	Drew *et al.* 1978

APPENDIX 1. (Continued)

	26	1400	Mature	268	25	293	Ogawa *et al.* 1965
	26	1200	?	144	16	160	Ogawa *et al.* 1965
	27	1147	Mature	238	24[i]	262	Sabhasri *et al.* 1968
S-dry forest	26	800	?	82	58	140	Jung 1969
	25.8	850	Mature	42	18[j]	60	Cintrón, unpublished data, Lugo *et al.* 1978
	26	1100	?	69	10	79	Ogawa *et al.* 1965
	24	603	Mature	28	12	40	Vyas *et al.* 1977

[a]T = Tropical, S = Subtropical.

[b]T = Mean annual temperature, P = mean annual precipitation; values obtained either from original source or from climate-diagram maps (Walter *et al.* 1975).

[c]The biomass of this component generally does not include stump roots, and therefore may be an underestimate.

[d]Mean of six plots (SE = 62).

[e]Estimated as follows: mean root/shoot for the tropical wet forests = 0.20. Organic-matter storage in roots was calculated by multiplying the aboveground organic-matter storage by the root/shoot ratio.

[f]Estimated as follows: mean root/shoot for T-moist forest = 0.17. Organic-matter storage in roots calculated as in footnote "e."

[g]Estimated as follows: mean root/shoot for the T-premontane moist forest = 0.16. Organic-matter storage in roots was calculated as in footnote "e."

[h]Mean of 36 plots; root biomass estimated from detailed analysis of 1 plot (r/s = 0.23).

[i]Estimated as follows: mean root/shoot for the S-moist forest = 0.10. Organic-matter storage in roots was calculated as in footnote "e."

[j]Estimated as follows: mean root/shoot for the S-dry forest = 0.43. Organic-matter storage in roots was calculated as in footnote "e."

APPENDIX 2. *Organic carbon content of soil.*

Life zone[a]	T[b] (°C)	P[b] (mm/yr)	Organic carbon (t C/ha)	Depth (cm)	Source[c]
T-rain forest	26.6	9000	367	76	Jenny 1950
T-premontane rain forest	22.1	5500	72	100	
	22.0	5500	71	100	
	19.5	5800	56	100	
	21.8	5500	52	100	
T-lower montane rain forest	13	4000	599	100	Edwards and Grubb 1977
	13.5	3750	214	100	
	13.8	3650	364	100	
	14.4	4400	252	100	
T-montane rain forest	10.8	2941	93	13[d]	
T-wet forest	22.5	4600	118	100	
	26.4	4300	73	100	
	27.7	4250	71	100	
	27.5	4350	82	100	
	25.8	5700	53	100	
	25.7	5700	92	100	
	25.9	5700	75	100	
	25.8	5700	103	100	
T-premontane wet forest	24.1	3600	255	100	
	26.2	3649	80	100	
	21.5	3300	155	100	
	21.8	3100	172	100	
	22.4	2950	108	100	
	22.5	2900	82	100	
	21.5	2800	452	127	Jenny 1950
T-lower montane wet forest	17.5	2900	193	100	
T-moist forest	27	3000	55	50	Folster *et al.* 1976
	27	3000	94	50	Folster *et al.* 1976
	27	3000	88	50	Folster *et al.* 1976
	28.1	2150	134	100	
	26.3	2250	75	100	
	26.3	2250	66	100	
	22.7	2500	100	100	
	24.5	2400	120	100	
	24.5	2400	76	100	
	25.0	2000	70	100	
	26.2	2100	85	50	Huttel and Bernhard-Reversat 1975
	26.2	2100	50	50	Huttel and Bernhard-Reversat 1975
	25.5	1807	69	100	Kira 1978
	27.2	1771	125	100	Klinge *et al.* 1975
	27	2700	75	100	Yoda and Kira 1969
T-premontane moist forest	25	1651	44	30	Greenland and Kowal 1960
	23	1850	190	100	
	25.5	1850	104	100	
	26.5	1800	35	50	Huttel and Bernhard-Reversat 1975

APPENDIX 2. (Continued)

T-lower montane moist forest	13.7	1450	170	100	
T-dry forest	27.3	1600	113	100	
	27.6	1550	97	100	
	27.8	1525	18	100	
	27.8	1525	57	100	
	27.8	1525	46	100	
	27.7	1525	90	100	
	27.6	1525	76	100	
S-lower montane wet forest	15	3000	80	40	Tanner 1977
	15	3000	250	45	Tanner 1977
	15	3000	90	40	Tanner 1977
S-wet forest	23	3450	73	30	Odum 1970
	19	2150	85	30	Brasell *et al.* 1980
S-moist forest	30	1100	65	50	Bandhu 1973
	22	1560	93	30	Brasell *et al.* 1980
	20	2070	188[e]	100	Chunkao *et al.* 1974, Lapudomlert *et al.* 1974
	30	1100	90	50	Singh 1979
	30	1100	46	50	Singh 1979
	30	1100	59	50	Singh 1979
	30	1100	45	50	Singh 1979
	20	2070	216[f]	100	Tannikij and Chunkao 1973
	26	1400	37	100	Yoda and Kira 1969
	26	1200	89	100	Yoda and Kira 1969
S-dry forest	26	1100	24	100	Yoda and Kira 1969

[a]T = Tropical, S = Subtropical.

[b]T = mean annual temperature, P = mean annual precipitation; both were obtained from original source or from climate-diagram maps (Walter *et al.* 1975).

[c]The sources are Holdridge *et al.* 1971, unless otherwise cited.

[d]Full soil profile, bedrock was below 13 cm.

[e]Mean of four samples; three were to 50 cm only (mean of these three = 154). We estimated the soil carbon to 100 cm in these three samples using the relationship: soil carbon in 50 cm = 80% of soil carbon in 100 cm (based on detailed data for total soil profile).

[f]Mean of 90 samples to 20 cm depth (mean = 97). We used the relationship that the top 20 cm = 45% of soil carbon in 100 cm (Chunkao *et al.* 1974, Lapudomlert *et al.* 1974) to estimate soil carbon content to 100 cm for the 90 samples.

APPENDIX 3. *Organic-matter storage in litter.*

Life zone[a]	T[b] (°C)	P[b] (mm/yr)	Litter[c] (t/ha)	Source
T-rain forest	26.6	9000	5.0	Jenny *et al.* 1949
T-lower montane rain forest	13	4000	7.7	Edwards and Grubb 1977
	13	4000	6.4	Edwards 1977
T-premontane wet forest	20	2300	4.8	Golley *et al.* 1975
	21.5	2800	16.5	Jenny *et al.* 1949
T-montane wet forest	12	1500	7.3	Brun 1976
T-moist forest	25	1800	5.5	Bartholomew *et al.* 1953
	25	1800	8.0	Bartholomew *et al.* 1953
	25	1800	7.3	Bartholomew *et al.* 1953
	26	2000	3.4[d]	Golley *et al.* 1975
	25	1800	5.6	Greenland and Kowal 1960
	25.5	1807	4.3	Kira 1978
	27.2	1771	11.3	Klinge 1975
	27.2	1771	6.0	Klinge 1976
	27.2	1771	7.2	Klinge *et al.* 1975
	26.2	3521	5.4	Klinge and Herrera 1978
	26.2	3521	7.2	Klinge and Herrera 1978
	26.2	3521	6.6	Klinge and Herrera 1978
	27	2700	1.8	Yoda and Kira 1969
T-premontane moist forest	25	1651	2.3	Greenland and Kowal 1960
	25	1650	5.3	John 1973
	20	1270	3.3	Malaisse *et al.* 1975
	20	1270	6.5	Malaisse *et al.* 1975
T-dry forest	26.5	1200	2.0	Madge 1965
S-lower montane rain forest	18.6	4500	4.4	Dugger 1978
S-wet forest	23	3450	6.0	Odum 1970
S-moist forest	30	1100	7.7	Bandhu 1973
	27	1147	6.5	Drew *et al.* 1978
	20.6	2000	9.7	Dugger 1978
	26	1400	2.6	Yoda and Kira 1969
	26	1200	3.0	Yoda and Kira 1969
S-dry forest	25.8	850	7.2	Lugo *et al.* 1978
	25.8	850	8.7	Lugo *et al.* 1978
	25.8	850	3.8	Lugo *et al.* 1978
	26	1100	3.4	Yoda and Kira 1969

[a]T = Tropical, S = Subtropical.

[b]T = mean annual temperature, P = mean annual precipitation; values obtained either from original source or from climate-diagram maps (Walter *et al.* 1975).

[c]Does not include large woody litter because only a few studies reported this value.

[d]Weighted mean (according to length of seasons) of dry and wet season values.

APPENDIX 4. *Primary production of tropical forest ecosystems.*

Life zone[a]	T (°C)	P (mm/yr)	Method[b]	Primary production: Gross (Pg) (t/ha yr)	Woody material	Above-ground	Below-ground	Total net	Source
T-premontane moist forest	20	1270	c	40.2	—	—	—	—	Bhandu *et al.* 1973
	26.5	1800	1	—	4.6	12.8	1.8[d]	14.6	Huttel and Bernhard-Reversat 1975
	20	1270	1	—	—	11.1	1.5	12.6	Malaisse cited in DeAngelis *et al.* 1981
	25	1651	1	—	11.2	18.2	2.6	20.8	Nye 1961
T-moist forest	26.2	2100	1	—	4.6	13.9	2.2[d]	16.1	Huttel and Bernhard-Reversat 1975
	26.2	2100	1	—	3.0	11.1	1.8[d]	12.9	Huttel and Bernhard-Reversat 1975
	26	3520	1	—	6.0	12.4	2.0	14.4	Jordan and Escalante 1980
	25.5	1807	2	68.7	5.2	12.7	5.5	18.2	Kira 1978
	27	2700	2	113.9	4.8	16.7	2.6[d]	19.3	Kira *et al.* 1967
	26	1900	2	50.2	7.5	9.6	1.5	11.1	Muller and Nielsen 1965
S-wet forest	23	3450	3	119.7	—	—	—	—	Odum and Jordan 1970
	23	3450	1	—	4.9	10.3	—	—	Jordan 1971
S-moist forest	30	1100	1	—	8.2	13.9	1.4	15.3	Bandhu cited in DeAngelis *et al.* 1981
S-dry forest	25.8	850	3/1	19.0	0.9	3.4	—	11.0	Lugo *et al.* 1978, Cintrón unpublished data

[a]T = Tropical, S = Subtropical.

[b]1 = Sum of increment of wood tissue and leaf, fruit and flower fall.

2 = Sum of respiration of plant parts, net increase in woody biomass and leaf and fruit fall; it does not include branch fall which authors included in their estimate (see text for explanation).

3 = Measurement of CO_2 gas exchange using an infrared analyzer; Pg = net daytime photosynthesis plus nighttime respiration. Net primary production = Pg − plant respiration (excluding root respiration).

[c]We were not able to determine from source which method was used (2 or 3); net = Pg − plant respiration.

[d]Estimated from average ratio of aboveground to belowground production for that life zone: 7.2 of T-premontane moist and 6.3 for T-moist, excluding Kira 1978 who estimated root production independently.

APPENDIX 5. *Litter production.*

Life zone[a]	T[b] (°C)	P[b] (mm/yr)	Litterfall (t/ha yr)[c] Leaf & fruit	Total	Source
T-rain forest	26.6	9000	—	8.52	Jenny *et al.* 1949
T-lower montane rain forest	13	4000	6.35[d]	7.56[d]	Edwards 1977
T-premontane wet forest	20	2300	—	10.48	Golley *et al.* 1975
	21.5	2800	—	10.20	Jenny *et al.* 1949
	22	4200	—	7.43	Kellman 1970
T-moist forest	24.7	2490	—	10.30	Bevege 1978
	27.2	1771	6.55	11.00	Fittkau and Klinge 1973
	27	3000	8.94	12.02	Folster *et al.* 1976
	27	3000	7.60	9.46	Folster *et al.* 1976
	27	3000	6.76	8.74	Folster *et al.* 1976
	27.2	1771	5.3	6.4	Franken *et al.* 1979
	27.2	1771	6.9	7.9	Franken *et al.* 1979
	26	2000	9.83	11.37	Golley *et al.* 1975
	26	2725	7.10	11.10	Haines and Foster 1977
	26.2	2100	8.10	9.18	Huttel and Bernhard-Reversat 1975
	26.2	2100	9.30	11.88	Huttel and Bernhard-Reversat 1975
	26.2	3521	6.14	9.54	Jordan and Escalante 1980
	25.5	1807	7.5	11.1	Kira 1978
	27	2700	—	11.8	Kira *et al.* 1967
	24.7	2277	8.6	9.9	Klinge 1977
	25.9	2277	8.2	9.0	Klinge 1977
	27.2	1771	6.0	7.4	Klinge and Rodríguez 1968
	25	1800	—	12.4	Laudelout and Meyer 1954
	25	1800	—	12.3	Laudelout and Meyer 1954
	25	1800	—	15.3	Laudelout and Meyer 1954
	25	1800	—	14.9	Laudelout and Meyer 1954
	26	2500	6.5	—	Leigh and Smythe 1978
T-premontane moist forest	26	1800	6.91	—	Cornforth 1970
	20	1600	8.76	—	Enright 1979
	23	1232	4.63	—	Hopkins 1966
	23	1987	7.17	—	Hopkins 1966
	26.5	1800	8.18	9.62	Huttel and Bernhard-Reversat 1975
	25	1650	7.80	9.66	John 1973
	20	1270	3.06	8.33	Malaisse *et al.* 1975
	20	1270	6.18	9.15	Malaisse *et al.* 1975
	20	1270	4.69	5.90	Malaisse *et al.* 1975
	25	1651	7.04	10.54	Nye 1961
T-lower montane moist forest	19	1800	—	7.8	Medina and Zelwer 1972
T-dry forest	26.5	1200	—	5.6	Madge 1965
	27	1334	—	8.2	Medina and Zelwer 1972
S-lower montane rain forest	18.6	4500	2.76	3.03	Dugger 1978
S-lower montane wet forest	15	3000	5.5	6.5	Tanner 1980b
	15	3000	4.9	6.6	Tanner 1980b
	15	3000	5.3	5.5	Tanner 1980b
	15	3000	4.4	5.6	Tanner 1980b
	19	2280	3.44	—	Bevege 1978
S-wet forest	20	2280	—	5.9	Bevege 1978
	20	2100	—	9.87	Brasell *et al.* 1980
	21	2400	5.55	11.65	Kunkel-Westphal and Kunkel 1979
	21	2400	7.81	9.33	Kunkel-Westphal and Kunkel 1979
	23	3450	7.73	10.02	Odum 1970
S-moist forest	30	1100	6.16	7.72	Bandhu 1973
	25.5	1680	—	9.0	Bevege 1978

APPENDIX 5. (Continued)

	22	1500	8.4	—	Bevege 1978
	20	2070	—	6.88	Boonyawat and Ngampongsai 1974
	22	1560	—	9.05	Brasell *et al.* 1980
	20.6	2000	—	5.48	Dugger 1978
	25	2000	—	10.0	Ewel 1976
	25	2000	—	9.0	Ewel 1976
	20	2070	—	4.55	Naprakob and Chunkao 1977
	20.4	1650	—	6.43	Rogers and Westman 1977
	30	1100	—	3.16	Singh 1968
	30	1100	—	4.20	Singh 1968
	30	1100	—	5.02	Singh 1968
	30	1100	—	6.20	Singh 1968
	30	1100	—	7.88	Singh 1968
S-lower montane moist forest	17	1566	4.62	—	Jackson 1978
S-dry forest	25	660	4.04	—	Garg and Vyas 1975
	26	800	2.5	4.5[e]	Jung 1969
	25.8	850	2.00	2.40	Lugo *et al.* 1978
	25.8	850	2.48	2.88	Lugo *et al.* 1978
	25.8	850	0.84	1.02	Lugo *et al.* 1978
	25	660	—	4.8	Ranawat and Vyas 1975

[a]T = Tropical, S = Subtropical.

[b]T = mean annual temperature, P = mean annual precipitation; values were obtained from either the original source or from climate-diagram maps (Walter *et al.* 1975).

[c]Excludes large wood fall.

[d]Mean of four plots, standard error = 0.1 (leaf and fruit) and 0.2 (total).

[e]Does not include the 7.1 t/ha yr of fruit and flower fall because the author suggested that it was not typical; high fruit production occurs only once during a many-year cycle.