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Carbon Dioxide Effects Research and Assessment Program

The Role of Tropical Forests on the World Carbon Cycle

MASTER

Report of a Symposium
Rio Piedras, Puerto Rico
March 19, 1980

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The Role of Tropical Forests on the World Carbon Cycle

A symposium held at the Institute of Tropical Forestry in Rio Piedras, Purerto Rico on March 19, 1980

Edited by
Sandra Brown, Ariel E. Lugo
and Beth Liegel

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PREFACE

Tropical forests constitute about half of the world's forest and are characterized by rapid rates of organic matter turnover and high storages of organic matter. For these reasons, and the impression that humans are using these forests at unprecedented rates, tropical forests are considered to be one of the most significant terrestrial elements in the equation that balances the carbon cycle of the world. In spite of this recognized importance, many scientists treat the tropics as a simple black box composed of a few forest types. Yet, as discussed in the paper by Tosi, tropical and subtropical latitudes are more complex in terms of climate and vegetation composition than temperate and boreal latitudes. The implications of the complexity of the tropics and the disregard of this complexity by many scientists is made evident in the paper by Brown and Lugo which shows that biomass estimates for tropical ecosystems have been overestimated by at least 100%. The paper by Brown shows that the rates of succession in the tropics are extremely rapid in terms of the ability of moist and wet forests to accumulate organic matter. Yet, in arid tropical Life Zones succession is slow. This leads to the idea that the question of whether tropical forests are sinks or sources of carbon must be analyzed in relation to Life Zones and to intensities of human activity in these Zones. The paper by Lugo presents conceptual models to illustrate this point and the paper by Tosi shows how land uses in the tropics also correspond to Life Zone characteristics. The ultimate significance of land use to the question of the carbon balance in a large region is addressed in the paper by Detwiler and Hall. They show how the cycles of cutting and subsequent growth alter the pattern and amount of carbon exchange between a region and the atmosphere.

A recurrent theme of the symposium was the difficulty of accepting certain generalizations that permeate the literature on the carbon balance problem. For example, the paper by Holdridge strongly argues in favor of mechanisms by which carbon flows from the terrestrial biota to the oceans, and thus allow forests to become net sinks of carbon because, once in the ocean, the return of CO_2 to the atmosphere is slowed down. He also questions previous interpretations of Mauna Loa data as does the paper by Lugo and Brown. In general, the symposium raised more questions than it answered. But, it does present the status of our inquiry into the role of tropical forests in the carbon balance of the earth.

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Rio Piedras, March 30, 1980

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ARE TROPICAL FOREST ECOSYSTEMS SOURCES OR SINKS OF CARBON?

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Introduction

Tropical forests affect the carbon balance of the world by: storing large amounts of carbon, doing so at a rapid rate, releasing carbon to the atmosphere through respiration, exporting organic matter to deep aquifers or oceanic ecosystems, or by their response to human uses which include the extraction of wood, forest destruction, or forest management for net growth. Those who believe that tropical forests are sources of carbon argue that rapid rates of deforestation reduce carbon storage and increase the amount of CO_2 going into the atmosphere due to burning and decomposition of vegetation (Woodwell et al. 1978). However, believers that tropical forest ecosystems are sinks of carbon emphasize the rapid rates of succession and high net CO_2 uptake of tropical forests (Broecker et al. 1979, Brown, this volume, and Holdridge, this volume).

A balanced view of the issue must consider both sides of the argument as depicted in Fig. 1 which is a diagram of land uses and their implications to the carbon balance. Climax forests (depicted on top of Fig. 1) are presumed to be in balance with respect to carbon uptake and release. More carbon is released than taken up when human or natural forces convert the climax forest into any of three possible states. The least disturbed is termed a successional forest, next is a clear cut or deforested area, and below it is an area dedicated to permanent non-forest use. Net carbon release to the atmosphere increases downward along this pathway of changing land use. Woodwell et al. (1978) assumed that this is virtually the only pathway operating in tropical regions. In fact, they assumed that 95% of the biomass in areas being deforested reached the atmosphere as CO_2 and that succession was negligible.

The left side of the diagram shows the successional pathway from disturbed forest to a climax state. Net carbon uptake characterizes this pathway. The rate of uptake depends on environmental conditions and speed of succession. Arid environments exhibit slow rates of succession, while humid environments exhibit much faster rates (Ewel 1977). Obviously, the secondary forest recovers quicker than the completely deforested site while land being dedicated to non-forest uses has little opportunity to act as a net carbon sink. The balance between the downward vs. upward changes in land-use dictate whether a tropical region is a source or sink of carbon. The objective of this paper is to explore with conceptual diagrams the forces and factors that may tilt the balance.

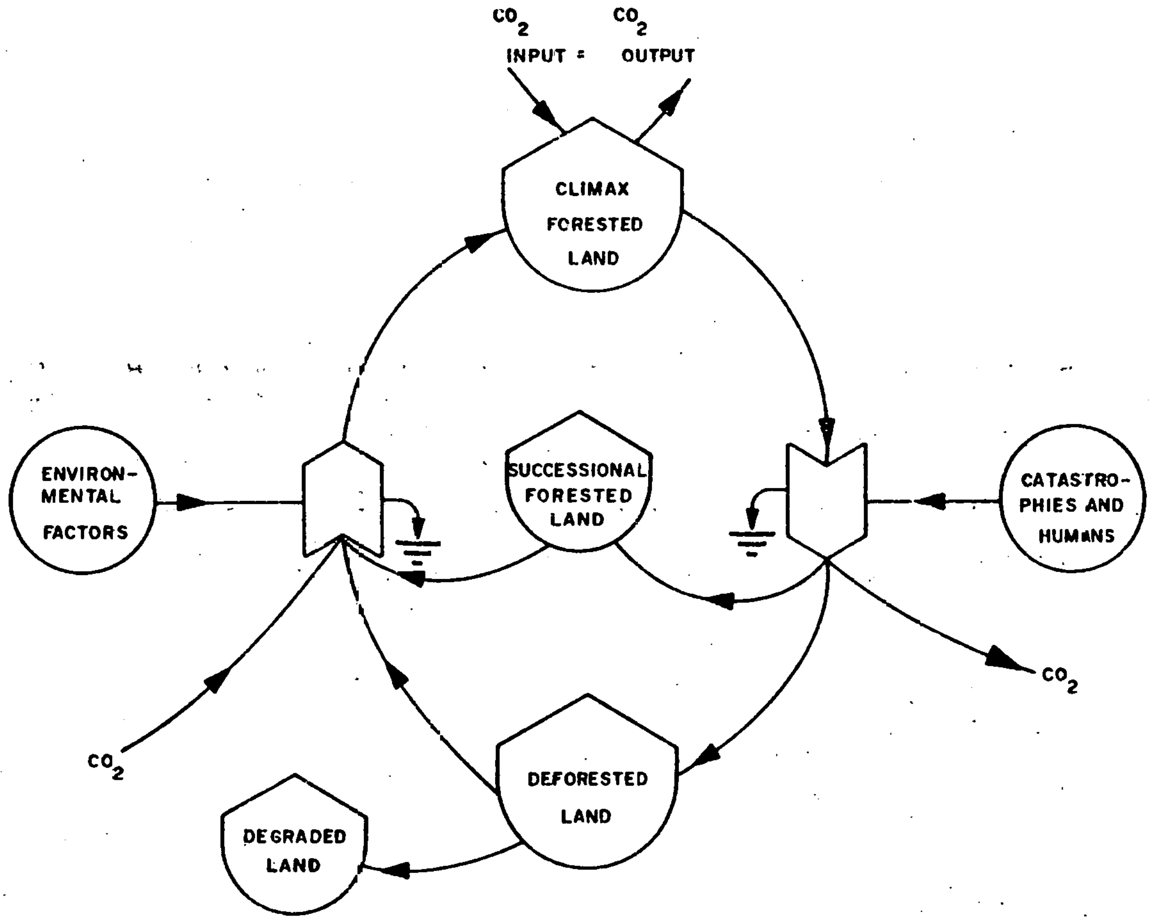

Fig. 1. Flow diagram illustrating land-use changes that affect the carbon balance. Deforestation leads to temporary carbon release which can be balanced by carbon uptake during succession. Circles represent the external forces that power either forest disturbance or forest regeneration. The lower tank (storages) represents lands that are not allowed to reforest and thus no successional change is shown. Arrows represent flows of material or energy.

Stable Steady State Condition

A stable steady state condition occurs when humans are completely dependent on solar energy for survival (Fig. 2). Under these conditions, humans are simple consumers and may use traditional shifting cultivation, hunting, or gathering as a means of procuring food. The carbon balance is maintained because the intensity of human activity is not high enough to offset the regrowth of vegetation. Succession easily takes up the CO_2 produced by the periodic clearing of vegetation.

The suggestion that a climax forest is in perfect carbon balance is a hypothesis that is yet to be proven correct. All ecosystems are open systems and thus they can never be expected to be perfectly balanced. Climax forests in the Luquillo Experimental Forest in Puerto Rico, for example, exhibited a small but measurable loss of dissolved organic matter to downstream ecosystems (Odum 1970). Odum measured up to 15 mg/l of dissolved organic matter in runoff waters during periods of heavy rains, but he only made four direct determinations. In a one-year study of watersheds in the lowland forests of Guatemala, Brinson (1973) measured high dissolved organic matter concentrations in rivers (up to 36.8 mg/l) and found these to be proportional to stream discharge.

High concentrations of organic matter in waters are usually associated with wetland ecosystems. For example, Brinson et al. (1981) reported that streams draining watersheds with extensive wetland systems exhibited dissolved organic matter concentrations of 3 to 72 mg/l while those that drained watersheds with few wetlands exhibited dissolved organic matter concentrations of 1.8 to 12.4 mg/l. Twilley (1980) found that black mangrove forests in Florida exported about 0.7 g organic matter $/m^2$.day. Yet, in terrestrial ecosystems, Lugo et al. (1978) measured a mean organic matter concentration of 115 mg/l in stemflow waters of a hardwood forest. Under a pine forest growing on sandy soils in Florida, organic matter concentrations in excess of 200 mg/l have been measured in ground water (E. Heald, Tropical BioIndustries Co., personal communication).

These data usually yield low absolute amounts of carbon when extrapolated to a global scale. The Amazon basin, for example, exports 0.2×10^{14}g carbon/yr based on dry season measurements of dissolved carbon concentrations and annual river discharge (Williams 1968). Yet, data show that even "balanced" ecosystems export organic matter to downstream aquatic ecosystems where carbon may be sequestered for long periods. The global significance of these exports still awaits elucidation because the data base does not permit a reliable calculation. For example, the calculation for the Amazon River is based on 12 determinations, none at high flood stage. For those rivers for which data are available, it is clear that export of organic matter is proportional to discharge (Brinson 1976; Fig. 3). Of more significance, however, are the unusual events that escape sampling. In Fig. 4 such an event is depicted for a river in Puerto Rico which discharged 70% of its annual sediment load and 10% of its annual water discharge in one day (Nov. 27, 1968). Until these events are taken into consideration, particularly in the wet tropics, it will be difficult to disprove the hypothesis that the flow of dissolved carbon through aquifers and rivers represents a significant global sink of carbon (Holdridge, this volume).

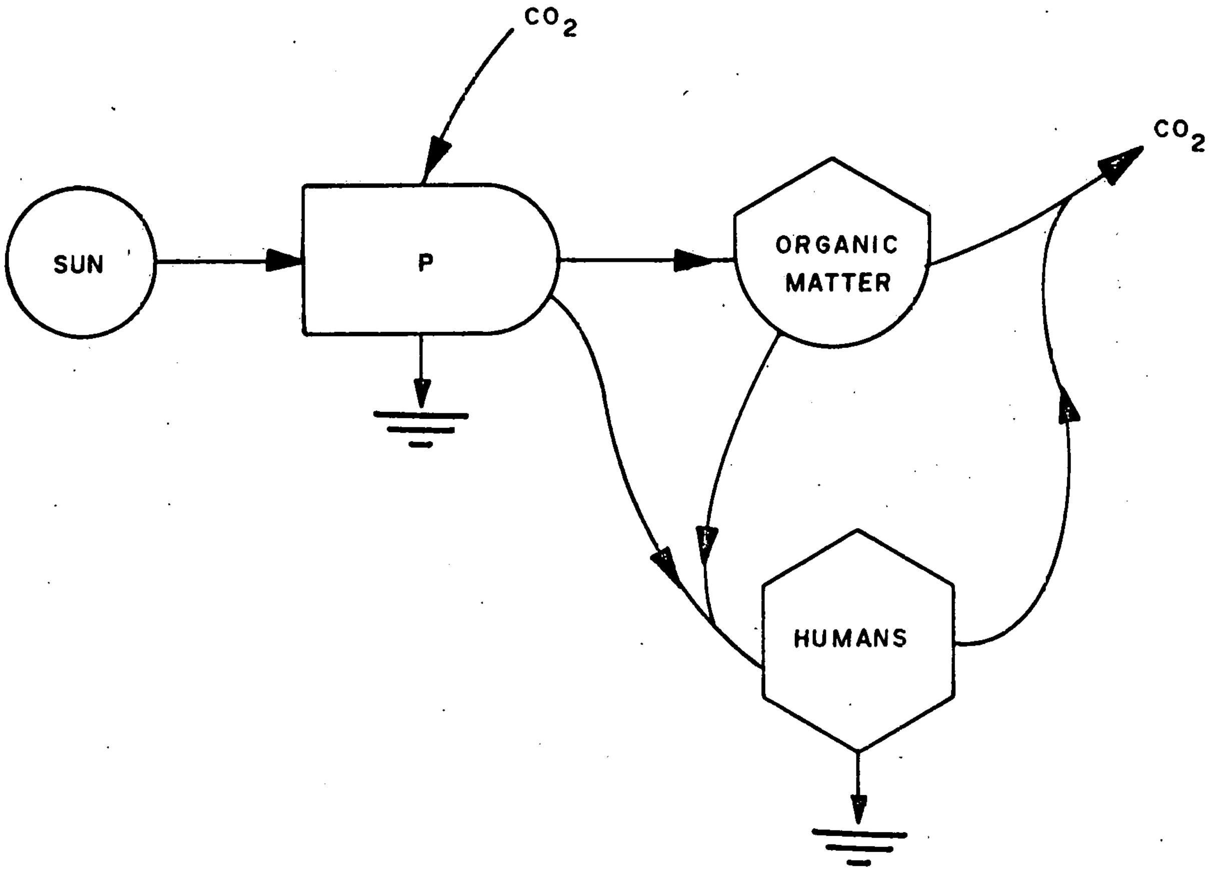

Fig. 2. Flow diagram of human use of natural forests when human activity is limited by solar energy. Under these conditions gains of carbon by photosynthesis (P) equal losses by respiration and combustion.

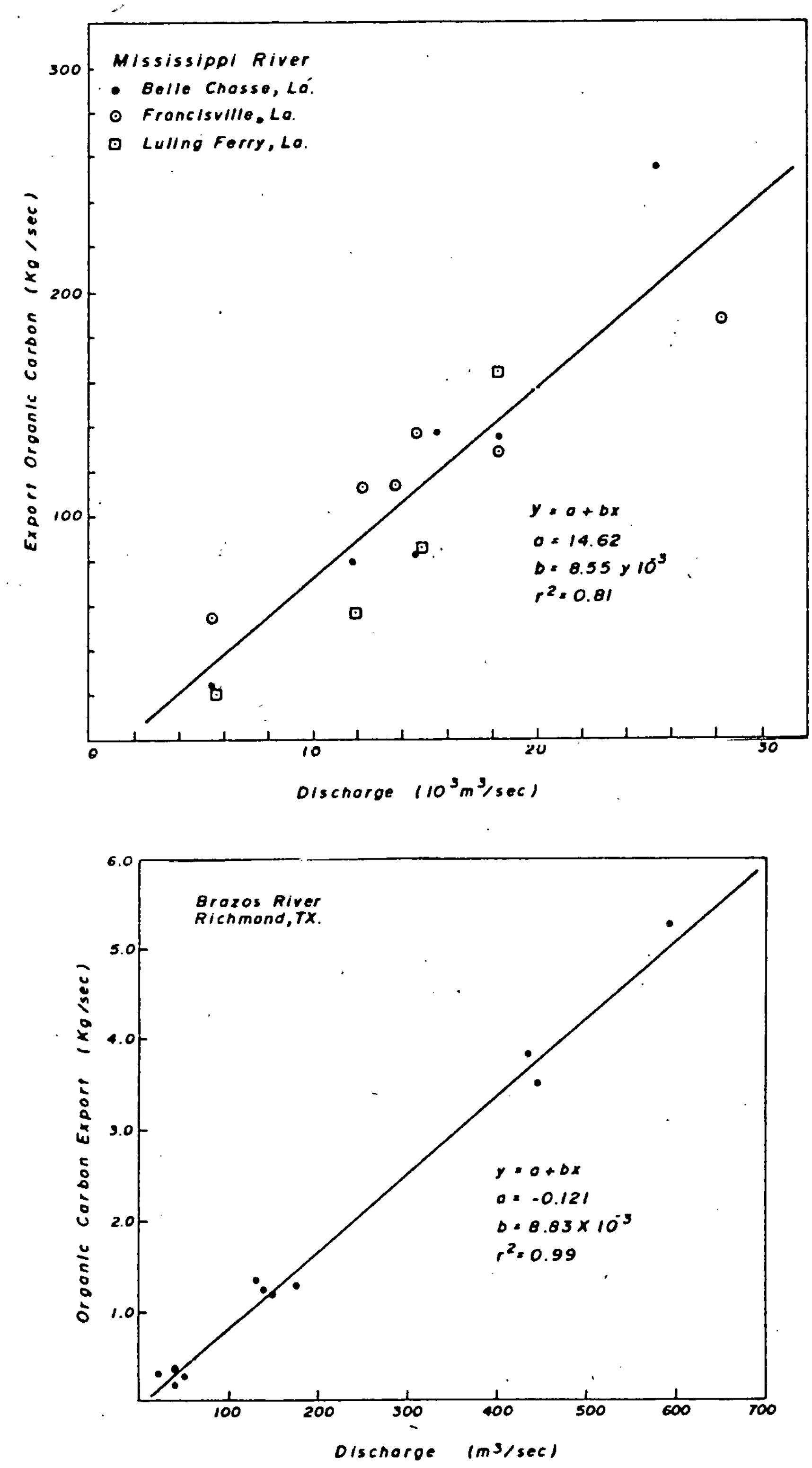

Fig. 3. Relationship between river discharge and export of organic carbon for six rivers in the U. S. (from Malcom and Durum 1976).

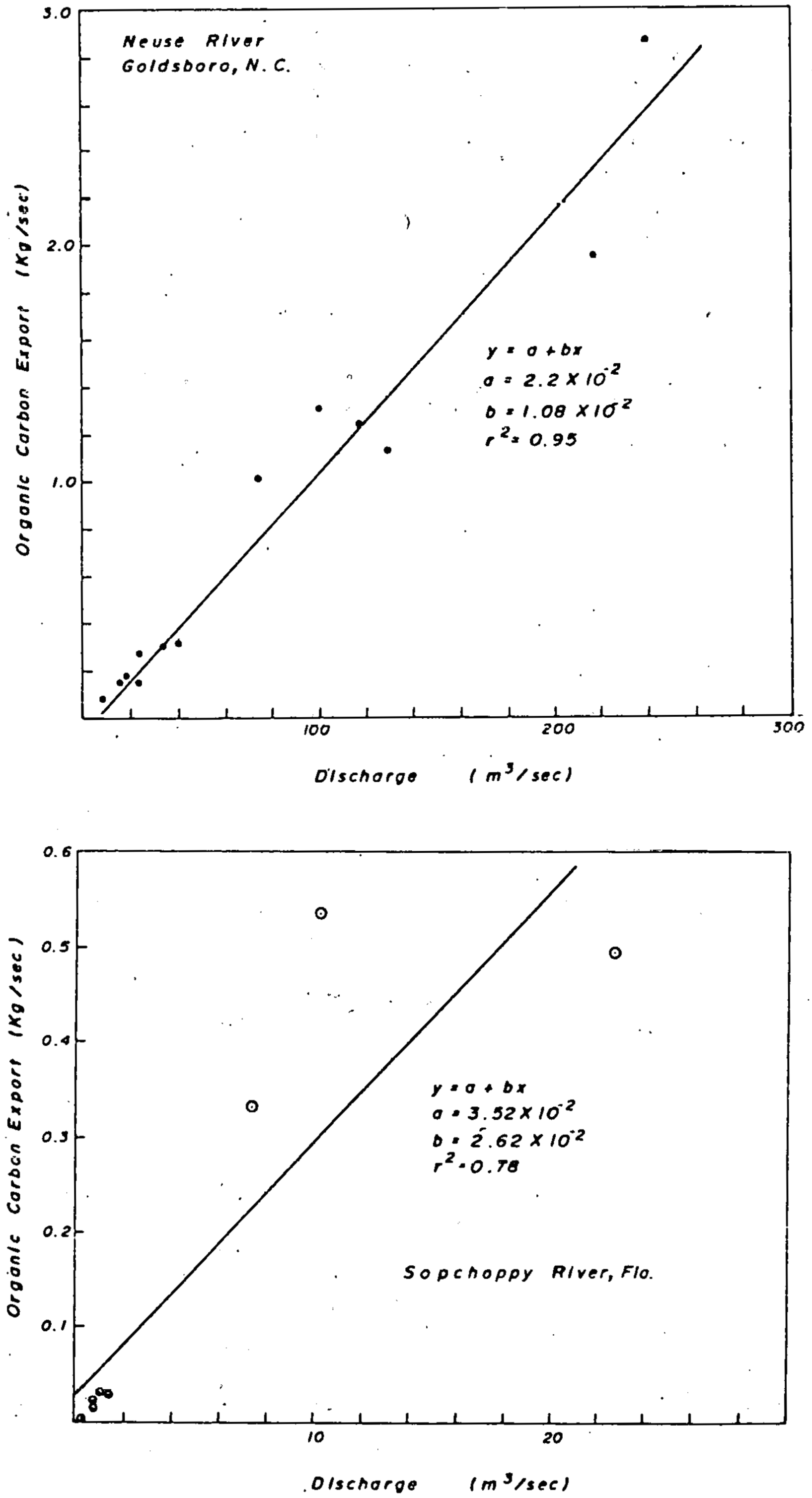

Fig. 3. (continued).

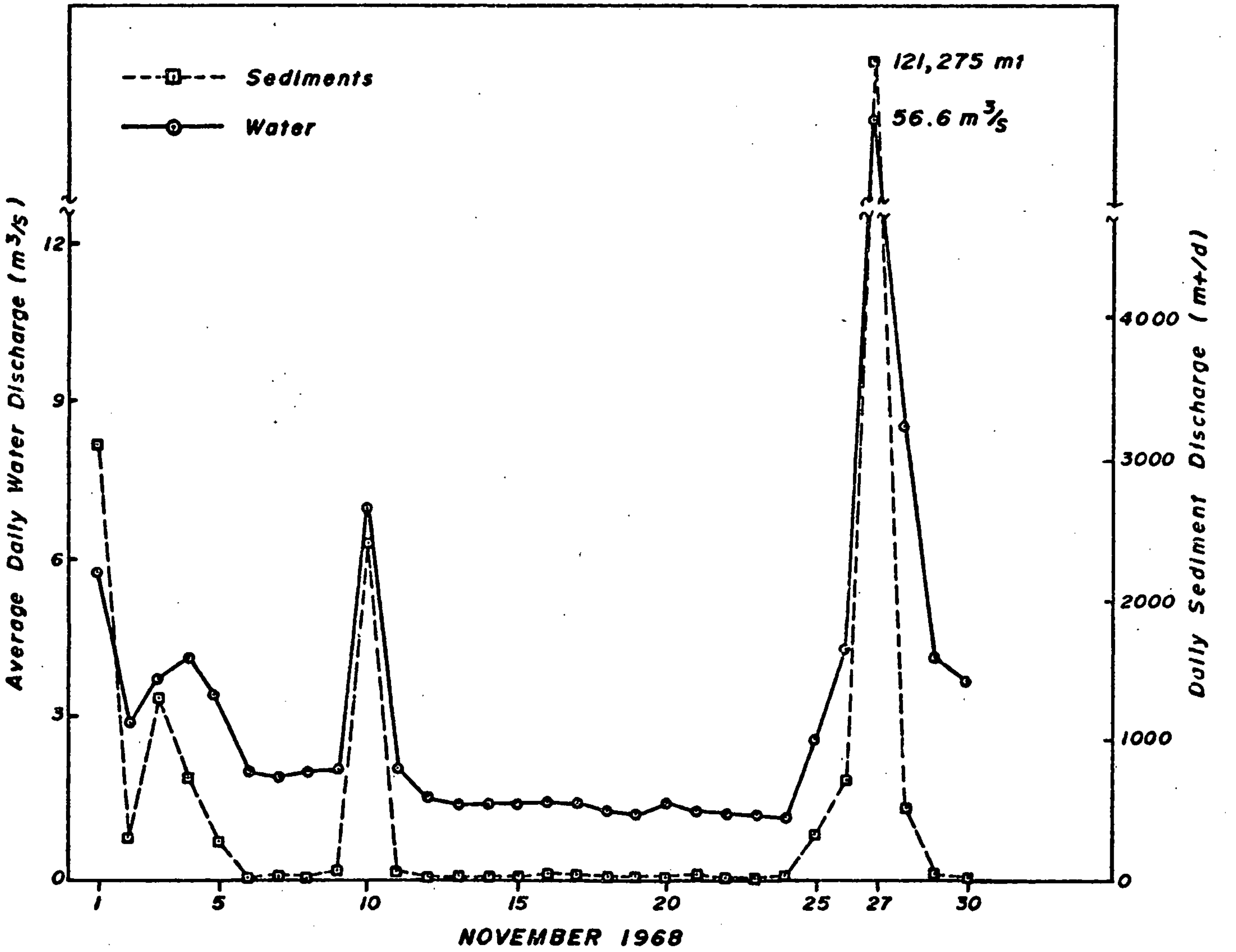

Fig. 4. Discharge and sediment export of Rió Tanamá in Puerto Rico for the period of November 1968 (Lugo et al. 1980).

Oscillating Carbon Uptake and Release Conditions

If humans have additional energy sources available, population densities can increase above natural carrying capacity and humans can exploit natural systems more fully (depicted in Fig. 5). I argue that this leads to long-term oscillations in terms of net carbon uptake or release by the landscape. Examples from two countries illustrate my point.

Tosi (this volume) has reviewed the land use changes in Costa Rica, a country that is entering a phase of rapid development of its lands because of increasing fossil fuel use. Deforestation is proceeding at fast rates and the country may be a net carbon yielder. In Table 1 I present similar data for Puerto Rico where deforestation occured much earlier, and where fossil fuels long ago replaced fuelwood as the main source of energy. Puerto Rico now has more forest resources than it did at the turn of the century. Apparently, the use of fossil fuels and the increasing dependence on imported food has allowed agricultural lands to go fallow and forests to return through rapid succession. Puerto Rico is now probably a net CO_2 sink as is the temperate region of the world where similar phenomena have occured (Armentano and Hett 1980).

Detwiler and Hall (this volume) suggest that land-use changes are the critical element in understanding the exchange of carbon between a landscape and the atmosphere. Puerto Rico and Costa Rica are examples of the two extreme points in a long-term oscillation in land-use that is a product of how humans use their fossil fuel energy and other natural resources.

Extreme Rate of Forest Exploitation

Under extreme rates of forest exploitation (Fig. 6) such as is happening in certain areas in the wet tropics (Tosi, this volume), large amounts of forest biomass may be converted to CO_2 but this condition may paradoxically lead to a sink of carbon because not all the biomass is converted to CO_2 (Ewel et al. 1980) and succession may be fast enough to support a vigorous young ecosystem with a rapid rate of net carbon uptake.

Another important consideration is that forest inventories in tropical countries normally include trees larger than 10 or 25 cm dbh while ignoring all smaller trees. Logging operations are also selective and leave behind enough trees to assure fast regrowth provided site quality hasn't been irreversibly affected (Ewel and Conde 1978). In fact, even in areas that have been cleared, tree regeneration and organic matter accumulation is extremely fast (Brown, this volume).

The fate of wood cut from tropical forests determines how fast that organic matter is returned to the atmosphere as CO_2. The production of roundwood in the world's forest is considerable (about 1.8 billion metric tons and increasing, Fig. 7) and tropical production accounts for about 40% of the total (Fig. 8a). However, over 70% of the world's charcoal and fuelwood production originates in the tropics (Fig. 8b). In biomass units fuelwood and charcoal production in the tropics is about 0.6 billion metric tons and increasing (Fig. 9). In terms of the roundwood production within the tropics over 80% is allocated for fuel wood and charcoal production (Fig. 10). This

Table 1. Forest areas and their carbon storage in Puerto Rico at different times in history.

Date	Forest Area ($10^3 km^2$)	Carbon Storage Equivalence[a] ($10^6 mt$)	Source
At the time of discovery (1493)	8.5[b]	93.8	Zon and Sparhawk 1923
1916	1.787	19.7	Zon and Sparhawk 1923
1950	2.352	26.0	Department of Natural Resources Inventory Program
1973	3.758	41.5	Department of Natural Resources Inventory Program

[a] Estimate for 1493 is based on Life Zone distribution given by Ewel and Whitmore (1973) and biomass storage in plants and litter from Brown and Lugo (this volume). For other years, estimates assumed equal rates of deforestation and growth for all Life Zones.

[b] Assuming 95% of island forested.

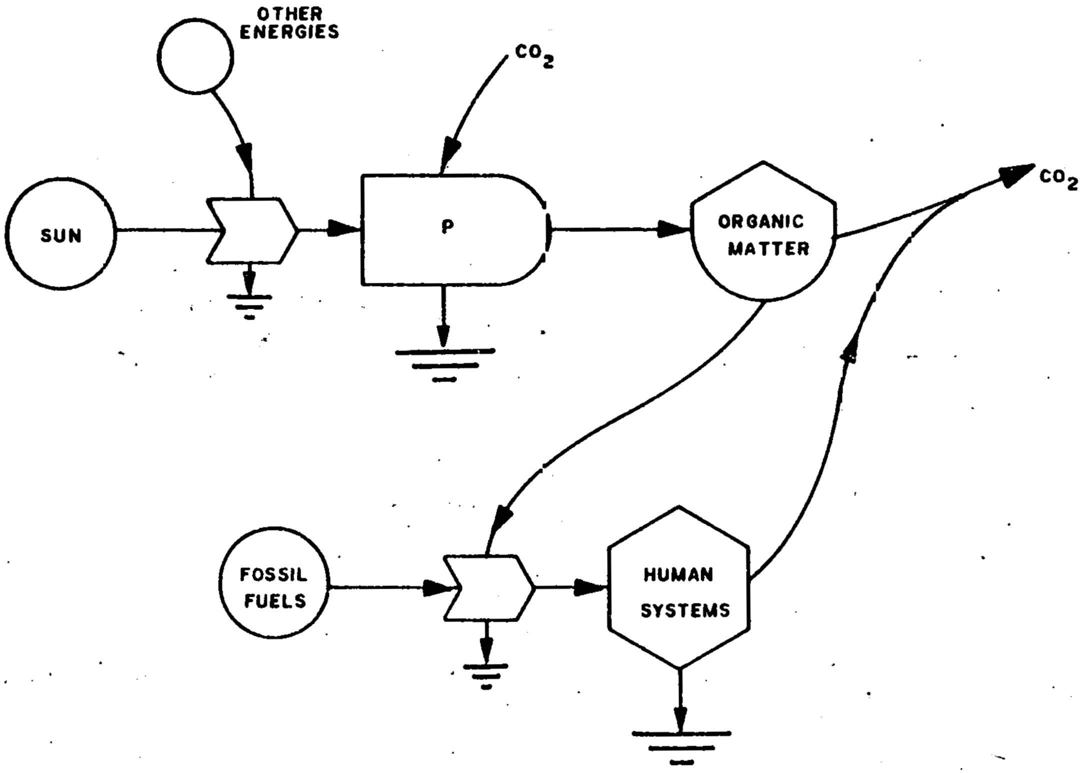

Fig. 5. Flow diagram of human use of natural forests when humans have access to fossil fuels. The additional source of energy allows an increased rate of forest exploitation or a substitution of forest products for fossil-fuel derived products. If environmental conditions are favorable, natural succession is rapid after disturbance. This leads to oscillations between forest disturbance (followed by net release of carbon to the atmosphere) and forest recovery (accompanied by net uptake of carbon from the atmosphere).

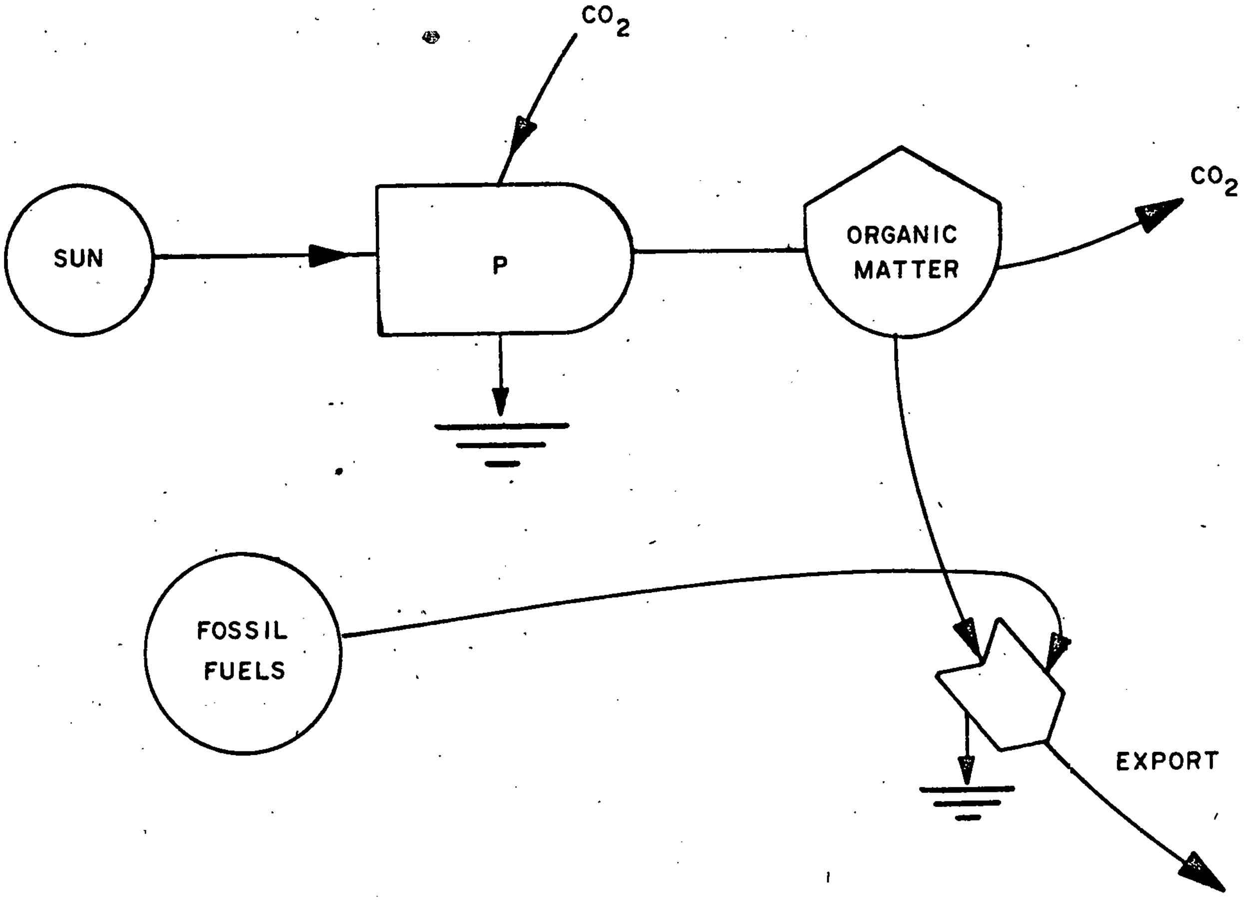

Fig. 6. Flow diagram illustrating the use of fossil fuels to rapidly exploit natural forests.

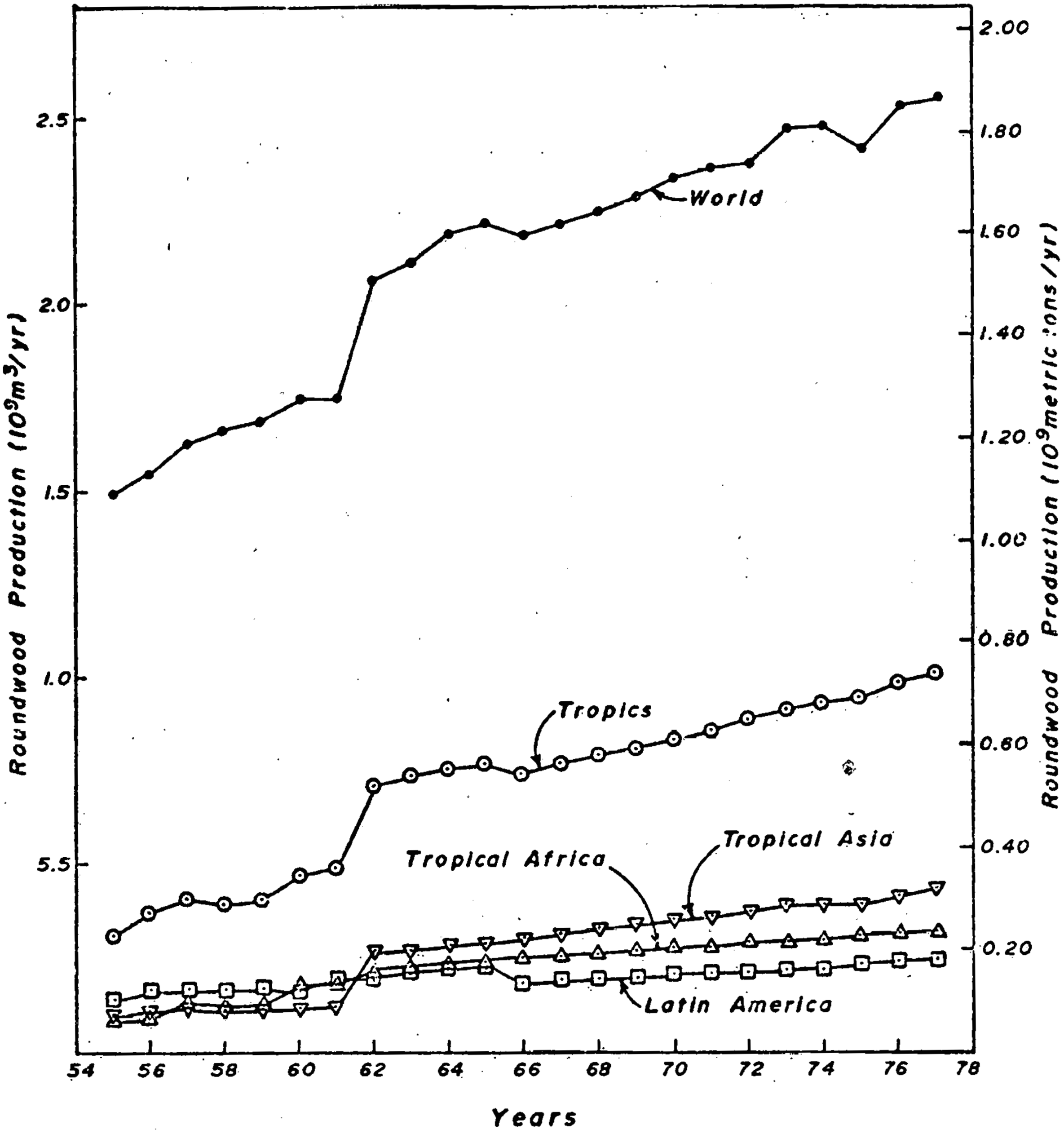

Fig. 7. Roundwood production in the world and the tropics (by continent) for the period of record (from Food and Agricultural Organization 1952-1963, 1973, 1977).

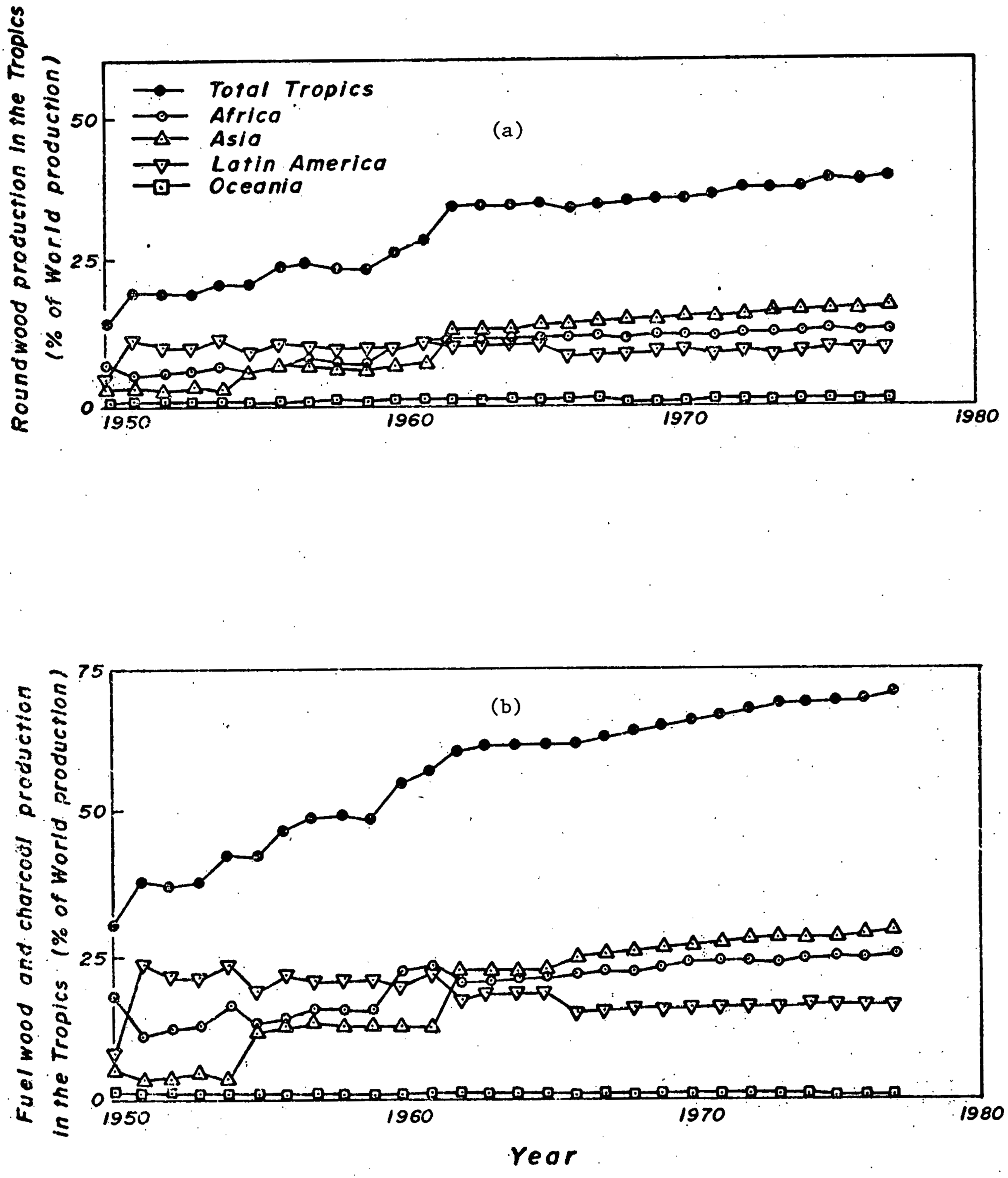

Fig. 8. Roundwood production (a) and fuelwood and charcoal production (b) in the tropics (by continent) as a percent of the world production for the period of record.

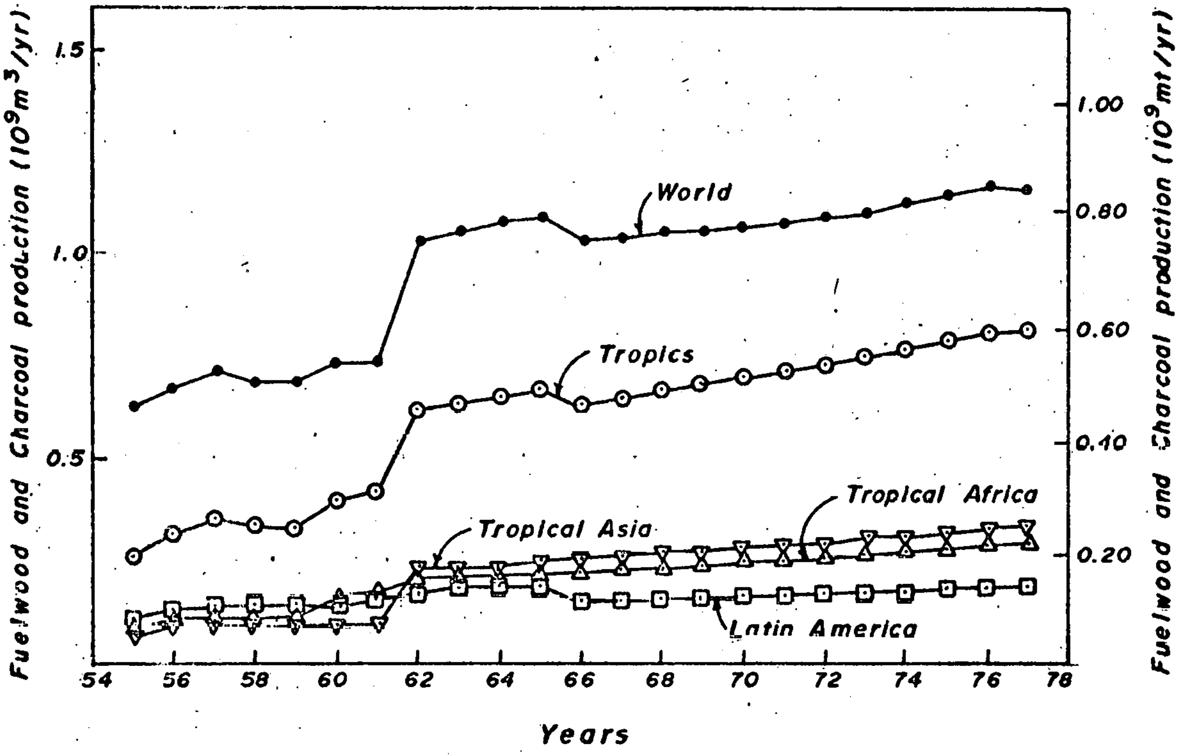

Fig. 9. Fuelwood and charcoal production in the tropics (by continent) expressed in biomass units for the period of record (from Food and Agricultural Organization 1952-1963, 1973, 1977).

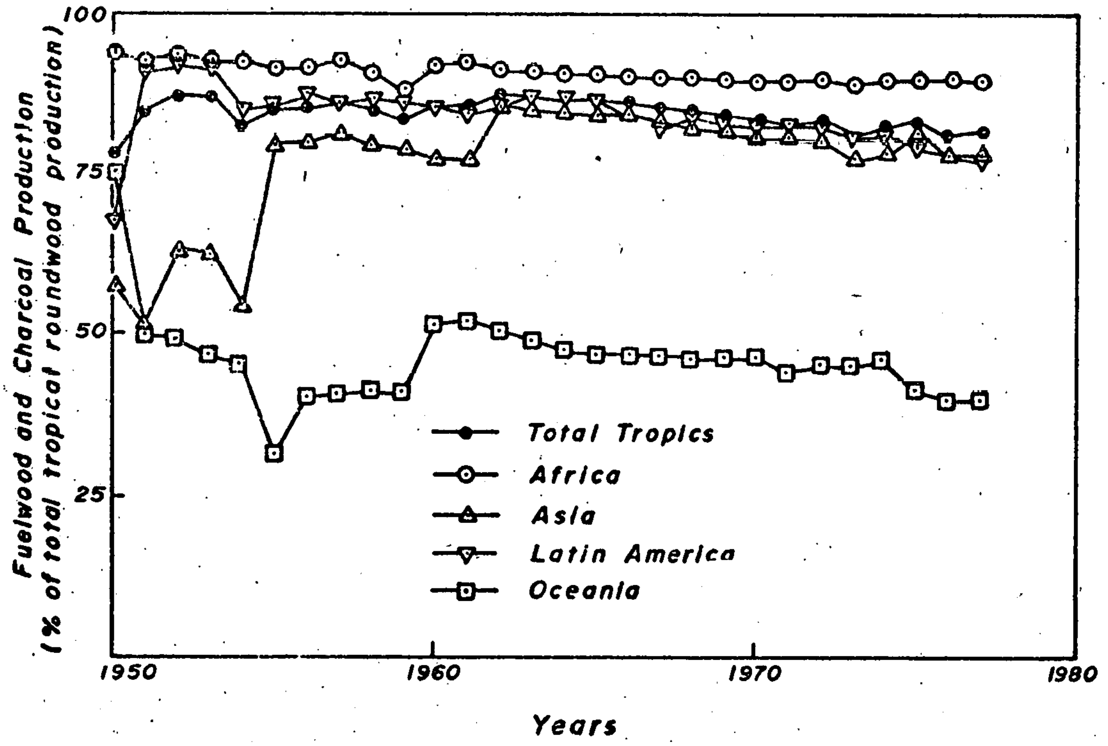

Fig. 10. Fuelwood and charcoal production in the tropics (by continent) expressed as percent of roundwood production for the period of record.

is true of most tropical areas except Oceania where forests are not well developed as they are in other tropical regions. These data suggest that tropical woods are predominantly used as energy sources and thus this biomass is rapidly returned to the atmosphere as CO_2 rather than remaining for long-term storage in structures or in other uses. Furthermore, the use of wood energy in the tropics may be more significant than these statistics reflect because of the large amount of wood that is used at the local level and not reported.

During traditional slash and burn activities, however, large quantities of wood remain on the ground where decomposition rate is extremely slow. For example, Ewel et al. (1980) reported that in Costa Rica, 40% of the original biomass remained on site mostly as soil organic matter and wood. Wood stumps decompose in humid environments at a rate of about 0.15 - 0.44 g/m^2.day (Odum 1970).

Declining States

In environments with natural stressors such as in very dry or cold regions, human populations subsidized by external energy sources could deforest the land irreversibly and thus create conditions that are clearly net sources of CO_2 (Fig. 11). In places like Haiti and the Sahel this must be happening. In these environments, succession is not fast enough to make up for human exploitation which is fueled by a growing population responding to external energy subsidies. Because of land devastation these areas hold little possibility for sustaining human populations in the future when cheap fossil fuels disappear completely.

Conclusion

I find it easier to find mechanisms and reasons why tropical ecosystems are sinks of carbon rather than sources. Paradoxically, even deforestation may create carbon sinks if succession is fast enough and if a portion of the initial biomass remains on site. Climax ecosystems may also be slow sinks of carbon via export of organic matter to downstream aquatic ecosystems. This pathway probably becomes more important in wet environments and in disturbed areas where the ecosystem may be more susceptible to leaching (Brinson 1976). The analysis of the Mauna Loa data by Lugo and Brown (this volume) also suggests that the biosphere acts as a sink of carbon as does the reasoning of Holdridge (this volume) based on the large carbon accumulations of the past.

In experiments with closed microcosms Odum and Lugo (1970) found that each microcosm reached and maintained a different "atmospheric" CO_2 concentration. This "atmospheric" balance depended on the relative proportions of plants and consumers in the microcosm. This lead to the speculation of the potential role of the biota in affecting such climatic phenomena as ice ages via the regulation of atmospheric CO_2. The current intense activity of humans, powered by abundant fossil fuels, is again tipping the world's carbon balance towards the production of carbon and possibly towards a warming trend in the world. However, there appears to be enough carbon uptake capacity in the terrestrial biota to slowly counteract this trend. In fact, one could hypoth-

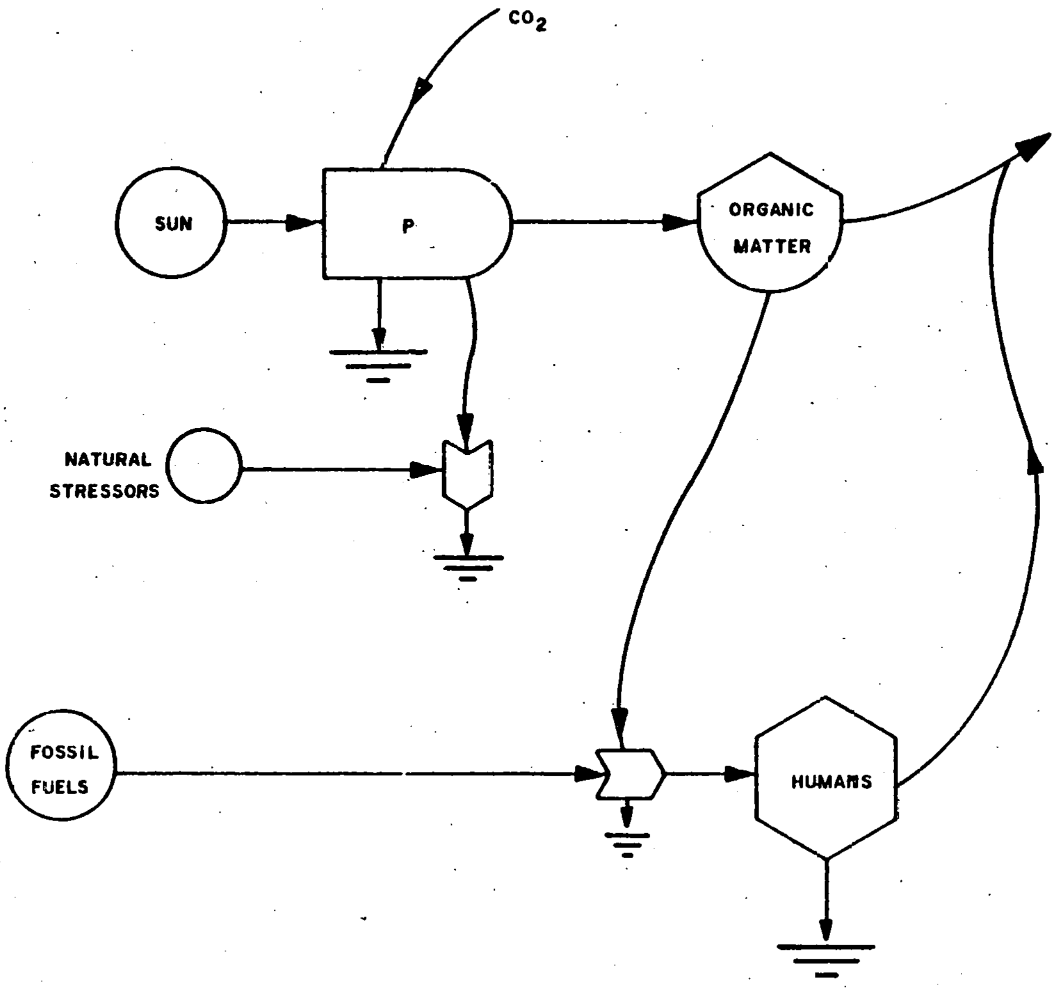

Fig. 11. Flow diagram of human use of natural forests when the forests are subjected to natural stressors and humans have access to supplementary energy resources. This situation leads to net carbon release because natural succession cannot keep pace with human use and thus the forest degenerates.

esize that, prior to the fossil fuel era, CO_2 in the atmosphere must have been decreasing since one of the analyses of the Mauna Loa data reflects a high rate of carbon uptake by the biosphere (Lugo and Brown, this volume). Proof is hard to come by, but the need for the missing information required to reach that state of understanding fuels our own interest in this issue.

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A NEW LOOK AT ATMOSPHERIC CARBON DIOXIDE

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Introduction

When I began to study the existing reports on atmospheric carbon dioxide (CO_2) with the intention of concentrating on the role of tropical forests in CO_2 movements, I found two puzzling or thought-provoking items in the proposed diagrams of the cyclic circulation of carbon (Baes et al. 1977, Ekdahl and Keeling 1973, Woodwell et al. 1978). One of these was an hypothesized annual balance or equilibrium between the incorporation of CO_2 in terrestrial vegetation through the process of photosynthesis and the return of an equal quantity of CO_2 to the atmosphere from the living and dead biomass of the same vegetation. The other item of special note was a lack of identification or even speculation about the specific origin and further movement of the tremendous amounts of carbon in the deep oceanic sediments and in the carbonate rocks formed from sediments in the past.

To a forester who has worked for several decades with plantations, the first item, that of a balance in movement of CO_2 from and back into the atmosphere, appeared quite unnatural. Wherever tree plantations are established on favorable sites and adequately tended, there is a continued annual increase in the volume of both standing wood and total biomass until heavy thinnings or harvest of the timber takes place. How can the proposed flows of carbon dioxide from and to the atmosphere possibly be in equilibrium?

Both second growth, following previous disturbance of a forest, and managed stands, after timer extraction, build up biomass in the same manner as plantations do, even though such forests are much more diverse in species and dimensions. Until maturity or harvest, carbon fixation in the increasing biomass of wood, living branches and roots is several times the magnitude of the carbon in the fallen leaves, decaying branchlets or roots, fallen bark, and an occasional dead tree. In general, outside of the lowland tropical regions, there is also a build-up of considerable litter and undecayed organic matter in or on the soil under such stands, in addition to the standing biomass.

Only in a virgin or mature, untended forest can one state with certainty that the average tonnage of carbon per hectare which oxidizies to CO_2 each year must be in balance with the quantity of carbon per hectare fixed by photosynthesis in an average year. However, virgin forests occupy an ever decreasing percentage of the land surface of our planet. Furthermore, there is no definite proof that all of the carbon dioxide from death and decay within mature or secondary forests returns directly to the atmosphere.

As averaged over several years, net photosynthesis and oxidation or decay to CO_2 probably are fairly well balanced in not only virgin forests, but also in forest areas subjected to swidden or shifting agricultural use, in areas of both annual and perennial crop agriculture, in pasture lands, in savannas, in natural bush-lands, and in deserts. On the basis of that rough estimate of balance, even if all oxidized carbon were to return directly to the atmosphere and the percentage of lands with CO_2 movements in equilibrium were to equal 75 percent or more of the earth's land surface, there would still be a considerable positive net flow of carbon from the atmosphere into the terrestrial biosphere. The latter would take place in forest plantations, in managed forests, and in long-term, second-growth stands such as those on abandoned farms in the northeastern USA, in Puerto Rico, and even in some places within the inner tropics. However, there are still two other items or activities which much be considered.

When a mature or any other appreciable forest cover is removed in the process of conversion to agricultural or pasture lands, a large part of the living biomass and the organic matter on or in the soil is either burned soon after cutting with the CO_2 entering the atmosphere directly or oxidized more slowly by decay over the next few years. Such a reduction in biomass by clearings has been going on for centuries, is practically complete in the temperate regions, and is only appreciably active now in the high rainfall areas in the tropics. In the tropical areas, in general, there is less biomass in the soil because the climate is not conducive to the accumulations of dead organic matter on or in the soil.

An appreciable counterbalance to this reduction of biomass in the process of land clearing consists of the long-term utilization of harvested timbers in the construction of buildings or other structures, as pilings, pit-props in mines, railway ties and many other items. Such uses postpone the decay of a considerable portion of the biomass produced in forest plantations or managed forests, as well as significant quantities from the tropical forest harvested either before or at the time of their being cleared. The data collected by FAO on timber exports are summarized here by Lugo, but it is of little help to draw conclusions because local uses of wood are not reported.

On the basis of the preceeding analysis, and supposing that all oxidized carbon returns quite directly to the atmosphere, one could deduce that either the movements of CO_2 between the atmosphere and the land biomass are balanced or that there is a small, but predominant movement from the atmosphere to the terrestrial biomass. Neither one of these deductions, however, offers the possibility that the terrestrial vegetation could serve as an annual sink for around three billion metric tons (Gigatons) of carbon entering and disappearing from the atmosphere each year as part of the addition to the air from the oxidation of the fossil fuels.

Thus, by supposing a prompt and complete return of oxidized carbon from the terrestrial biomass to the atmosphere, one is effectively eliminating living land vegetation as a possible sink of excess CO_2. The only other possible sink, namely the oceans at their interface with the atmosphere, is one of simple movements of CO_2, an hypothesis which appears to have been justifiably discarded by most scientists because of the lack of positive evidence of any significant net movement into the ocean. Models of oceanic systems suggest that the uptake capacity of the oceans is about 2 billion metric tons of carbon (Broecker et al. 1979).

Finally, there is one other piece of factual evidence which challenges the belief of a rapid return to the atmosphere of all the oxidized carbon, so as to effectively balance net photosynthesis. That evidence consists of the geological knowledge that tremendous quantities of organic matter accumulated in the past from virgin forests of even simpler composition and probably slower growth than those of the present. Those accumulations of matter were converted subsequently by heat and pressure into the deposits of coal which we are now extracting from the earth. Seemingly, if there could have been a large surplus production of wood and other organic matter in the virgin forests of the past, the same possibility should exist today for a surplus production of carbon from the terrestrial vegetation. Nevertheless, none of this evidence is acceptable as long as atmospheric gas analysis values are interpreted as signifying balanced movements of carbon between the atmosphere and land vegetation.

With a presentiment that the terrestrial vegetation has to be the main sink for carbon dioxide from the atmosphere, a close examination was made of the CO_2 concentration of the atmosphere throughout the year as measured at Mauna Loa, the South Pole and Point Barrow, Alaska. Values plotted in the diagrams as shown in Fig. 1 are monthly averages of parts per million (ppm) by volume of CO_2 in the atmosphere. The diagrams clearly show continuously decreasing monthly values from around March to late fall and successively larger values from the latter time until the high in the spring.

The decrease from spring to fall is supposedly due to the predominance of photosynthesis over respiration with the vegetation drawing CO_2 from the atmosphere whereas the increase from fall to spring would be due to net respiration or oxidation of carbon with a release of CO_2 to the atmosphere.

From a forester's point of view, the long continued seasonal increase in net photosynthesis does not look correct because in the north temperate and boreal regions, tree growth is active only in spring or early summer. Likewise, I find it difficult also to visualize a steady increase in the values of net oxidation or decay of organic matter right through the cold, winter season.

The lag in net photosynthesis into the fall at Mauna Loa is explained in the literature as due to the lapse in time of general atmospheric movements from east to west, from North America to Hawaii. That supporting argument is hard to challenge, because any such large-scale atmospheric movements are surely complex and variable.

At Mauna Loa, a continuous gas analyzer was utilized, whereas almost all of the data from the South Pole comprised those from subsequent laboratory analyses of samples collected in flasks on schedule. For a one-year period,

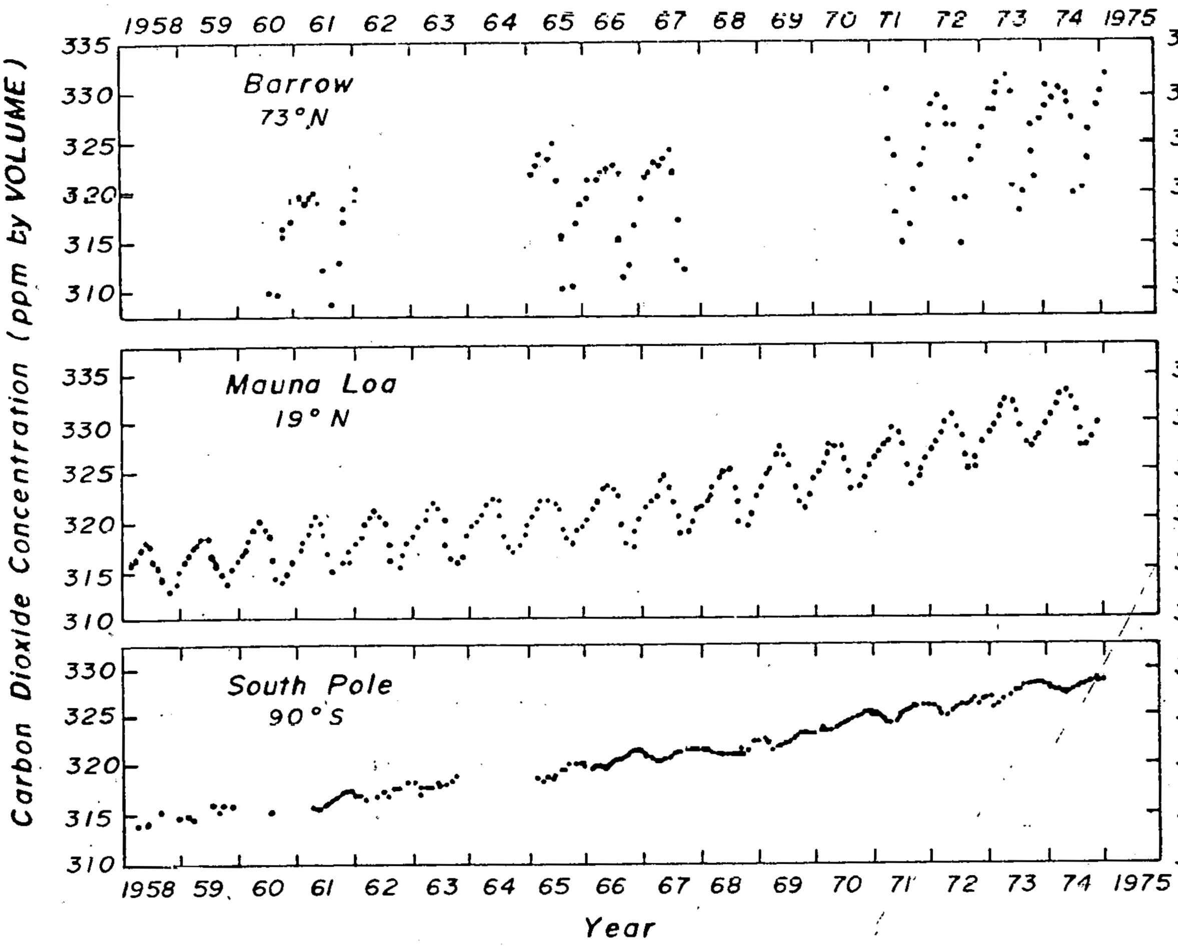

Fig. 1. Atmospheric CO_2 concentrations for Point Barrow, Alaska (top), Mauna Loa, Hawaii (middle), and South Pole (bottom) monitoring stations (from Machta et al. 1977).

South Pole data were from a continuous gas analyzer. As the values from the latter showed the same pattern and magnitudes as those from the flask samples, one may be quite certain that both methods give equivalent readings.

An important item to remember is that the analyses were intended to determine the parts per million (ppm) of CO_2 by volume. In other words, a reading of 316 ppm by volume implies that in 1,000 liters or 1,000,000 cubic centimeters of atmosphere at a given temperature and pressure, there should be 316 cc of CO_2. Because of Avogadro's Law, one can say that the above is equivalent to having a molecular density of 316 molecules of CO_2 in a sample of atmosphere containing a total of one million molecules.

If pressure were increased on the preceding volumetric sample, so that the atmospheric gases of the sample decreased in volume to one half or 500 liters, the CO_2 would then comprise only 158 cc, but would still be 316 ppm by volume. In reverse fashion, if the original sample was joined to another container of 1,000 liters filled with a vacuum and allowed to expand, the CO_2 would then occupy 632 cc of the total volume of 2,000 liters, but again would comprise only 316 ppm by volume.

Because the pressure and temperatures of given volumes of gas in containers are correlated, the compressed gas in the previous examples would become warmer whereas the expanded gas sample would cool. Supposedly, samples from the atmosphere or from flasks could be compared with calibrated samples prepared in a laboratory, if both were subjected to the same pressure or rate of flow and the same temperature. Readings were apparently made in accordance with the density of CO_2 molecules, wherein the correlation of Avogadro's mole with molecular density gives parts per million with no problems.

There appears, to me, to be one possibility for error in the ppm readings of CO_2 in the atmosphere. That, I believe, is due to the lack of uniform correlation of the density of the CO_2 molecules with pressure in the open atmosphere. This is quite distinct from laboratory observations and laws.

The pressure of a gas within a closed container in the laboratory increases in direct correlation with an increase in temperature of the gas. As the temperature rises, the gas molecules move more rapidly and thus exert a greater pressure on the container walls. In the open atmosphere, on the contrary, the pressure of the atmospheric gas is due to its own weight or to the gravitational attraction between the earth and the atmosphere. Rises in the temperature of the atmospheric gas produce the same speed-up of gas molecules, but the result is an expansion of the gas mixture rather than an increase in pressure.

At sea level, where the pressure of a column of air in warm weather may be exactly the same as that in the winter, the density of the gas molecules per cc would be less in the summer than in the winter due to the expansion of the air column with the heat of summer and the contraction of the air with the low temperatures in winter.

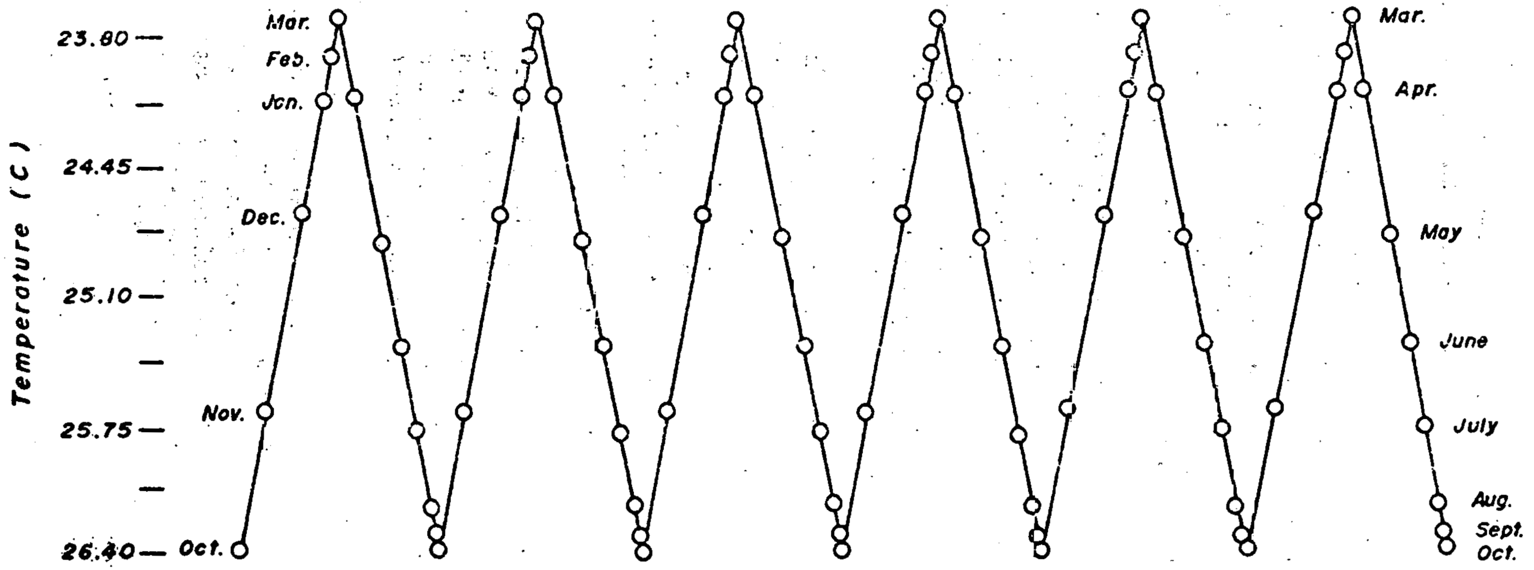

Fig. 2. Average monthly mean temperature of surface oceanic water temperatures taken off-shore to the Northeast of the Hawaiian Islands at latitude 20.9°N longitude 156.0°W plotted repetitively to approximate several-years pattern.

All this in no way changes the gas laws. It simply indicates that a gas analyzer cannot correctly compare the gas composition in an open planetary atmosphere with that of calibrated container gas samples without the application of a correction factor due to the general atmospheric gas temperature at the time of sampling.

The CO_2 readings in ppm from gas analyzers should be correlated with general hemispheric temperatures of the atmosphere. However, due to local alterations in air flow and temperature within the atmosphere, a clearer correlation may be obtained from marine surface water temperatures. The lags in heating in the summer and cooling in the winter of the surface waters off-shore from Maui in the Hawaiian Islands, as shown in Fig. 2, correspond very well with those of the previously reported highs and lows of CO_2 ppm in the air.

The preceding interpretation of the plotted CO_2 atmospheric readings does not alter the fact of a steady annual or semi-annual (secular) increase of CO_2 in the atmosphere of our planet. Carbon dioxide is still building up in concentration in the air. However, the proposed interpretation of the seasonal zig-zags does remove the restriction on our understanding of the carbon cycle which had been imposed by a presumed balanced movement between the atmosphere and the terrestrial biomass. In other words, the terrestrial biomass may be considered as a possible sink for atmospheric CO_2.

If one accepts the idea of terrestrial vegetation being an appreciable sink for CO_2 from the atmosphere, he is immediately confronted with a new problem, namely: If the land vegetation is absorbing in net photosynthesis about 1 to 3 G-tons per year of the carbon being added to the atmosphere from the burning of fossil fuel, plus a lesser but unknown amount from man's clearing and burning of forest cover, over and above that consumed in growth of the existing vegetation, then one must explain where the excess carbon goes after being fixed temporarily in the vegetation.

Obviously, the most elegant solution to the above disappearance of carbon after it had been fixed in terrestrial vegetation would be to have it released from the vegetation by decay and moved gravitationally by percolation of waters into the ground or stream runoff from the soil to the depths of the oceans. This would account for deposits of carbon in sediments or carbonate rocks made from sediments.

The problem one encounters with the preceding hypothesis is that there is extremely little supporting evidence available. However, evidence is normally gathered to prove or disprove a hypothesis so that a lack of evidence may be in part due to the past lack of a supposition that carbon was moving in appreciable quantities from the atmosphere into the land biomass and from there via fresh water streams to the ocean and its depths. In other words, if one is sure that all the carbon derived from the atmosphere in net photosynthesis of land plants soon returns to the air following death and oxidation of the organic matter, he is not going to waste his time checking other possible dispositions of the CO_2 from the oxidation.

Furthermore, the necessary direct evidence may not be easy to obtain. The volume of fresh water moving into the ocean each year while huge, is relatively small compared with the total cubic content of the oceans. The tonnage of ocean sediments and sedimentary rocks which appears so impressive could have been accumulated with relatively small annual increments over hundreds of millions of years. Then, too, we must remember that only within the last few decades has vegetation clearing been pushed up to large figures and the burning of fossil fuels reached impressive volumes.

As an example of a negative opinion, namely one against the hypothesis of an appreciable carbon movement from land vegetation to the sea, Riley (1973) wrote: "The non-living organic matter is derived from living organisms in the sea except for a small and probably insignificant amount from terrestrial sources, and the ultimate source is, of course, photosynthetic fixation of carbon in the surface layer." However, there is very likely a need for more selective sampling of fresh water moving to the oceans before writing off the effect of land vegetation sources as Riley did.

For example, the deposits of coal were almost completely laid down in temperate climates. This localization must have been due to what is termed a rapid turn-over of organic matter in the tropics as opposed to a much slower decomposition of organic matter in the temperate regions. We do not know what percentage of the organic matter in these two regions goes back to the atmosphere and what percentage may go to the sea. When examined carefully there appears to be some strong reasons for supposing that a considerably larger part of the carbon of the tropical forests could move directly to the sea.

The main reason for the latter belief is due to the generally higher rainfall in the tropics than in the temperate regions. The greater annual precipitation in the tropics not only produces a greater movement of water over and through the soil, but also limits root penetration to a lesser depth for lack of aeration. Higher average temperatures throughout the year coupled with the greater moisture in the soil favor rapid decomposition in the tropics.

Furthermore, one should not just consider the tropics as a whole as a probable theater for CO_2 movement to the sea, but rather concentrate on those moister areas which are usually lumped together by temperate zone ecologists and plant geographers as the tropical rain forest. Even there, the rivers during the dry season are usually clear and much reduced in volume. In order to be sure that there is not a considerable movement of dissolved and particulate carbon down the streams to the sea, samples of flowing water should be taken following heavy rains and especially so during the several-day storms of peak rainy season when there is complete saturation of the soils and flooding of the recent and some of the older alluvial terraces along the streams (see the paper by Lugo in this volume).

Not only are the storm periods unpleasant times in which to be taking samples, but they can also be dangerous. In addition to the probability that the waters are carrying much dissolved or particulate carbon, it is obvious that the swollen, fast-running streams are carrying branches, logs, and even sometimes entire uprooted trees. I remember once rains of 330 mm in one day in Puerto Rico, when the entire width of the Luquillo Mountain highway slid away in a couple of places. I have also been in forest with water several meters above the normal level of the Río Puerto Viejo in Costa Rica and watched river fish scurrying around in the shallow water between the trees in their search for a short time bonanza of extra food during a flood peak. It is hard to believe that all of the precipitation of the heavy seasonal rains and of the occasional storm periods are not flushing out and dissolving or carrying along with their waters very appreciable quantities of carbon for the organic sediments.

Thus, although we still do not know the quantitative details of the carbon cycle on our planet, I believe that we do know enough to understand the general picture. Although many have imagined a rather grim picture of a CO_2 build-up in the atmosphere, a resultant warming of the earth's climate with a melting of polar ice and covering of extensive low elevation areas, the years will probably show that the situation will not be that serious.

More likely, as man slows down the rapid clearing of forests for other uses primarily because the remaining mature forest areas are now limited in extent and, on the other hand, increases both the area of managed forests and the long-term utilization of forest products from those forests, the existing vegetation will be able to absorb a higher percentage of the CO_2 being released from fossil fuels. Even the Organization of the Petroleum Producers, without doing so because of CO_2, is giving signs of serious attempts to slow down the extraction and use of the fossil fuel, petroleum.

Figure 3 is my diagram of a proposed carbon cycle which indicates a definite partial movement of carbon from the terrestrial vegetation through decay and oxidation to the seas thus providing a hypothetical source for the large deposits of marine sediments of carbon and the carbonate rocks. Also indicated is a hypothetical route for the return of the carbon of those rocks to the atmosphere through the processes of superimposition of a moving plate of the earth's crust by another, melting of the rock within the earth, followed by ejection of ash or lava and CO_2 from volcanoes. That would leave open for speculation the possiblity of past and future appreciable variations of CO_2 in the atmosphere.

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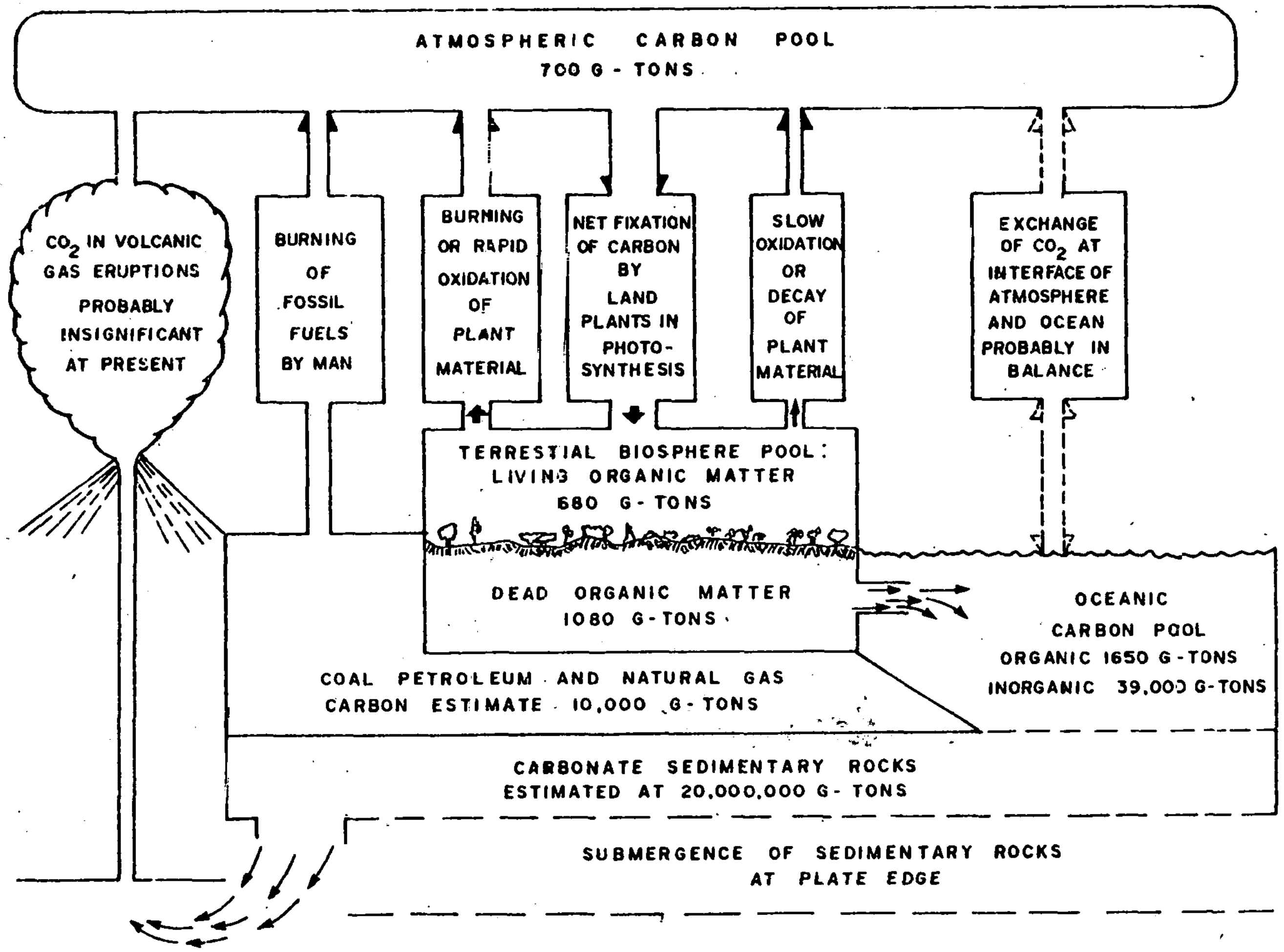

Fig. 3. Planetary Carbon Cycle. Values of the carbon storage in the various pools are from Baes et al. 1977 and Reiners 1973.

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ECOLOGICAL ISSUES ASSOCIATED WITH THE INTERPRETATION OF ATMOSPHERIC CO_2 DATA

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Estimates of whole ecosystem metabolism from atmospheric CO_2 data were made by Woodwell and Dykeman (1966) who capitalized on atmospheric inversions to calculate total forest respiration rates. Hall et al. (1975) used the extensive Mauna Loa data to estimate "net hemispheric metabolism". In these calculations they corrected the Mauna Loa data for the presumed CO_2 uptake by oceans and used the seasonal change in atmospheric CO_2 concentration as a measure of net CO_2 release or uptake by the vegetation. Their technique is similar to established procedures in limnology or terrestrial ecology for analyzing dissolved oxygen or CO_2 exchange diurnal measurements. However, because of the oceanic correction applied to the data, their analysis only reflects the metabolism of terrestrial ecosystems. Furthermore, their analysis was limited in scope because it only looked at the annual changes in CO_2 uptake or release and failed to discuss a number of ecological issues that require resolution if we are to make progress in the interpretation of global ecosystem processes. In this paper we raise these issues. Atmospheric CO_2 concentration data are not corrected for oceanic exchange and the data are analyzed on a monthly basis. By doing so, hemispheric metabolism is estimated with more resolution. In the analysis of results we address questions about the seasonal patterns of hemispheric metabolism, correlate the time of peak metabolic activity with what we know from ecosystem measurements, examine the ratio of CO_2 uptake to CO_2 release by the hemisphere as a whole, and examine the data as one would examine CO_2 diurnals to see if the magnitudes of CO_2 uptake and release check with those derived by others using different methodologies.

Methods

Updated atmospheric CO_2 concentration data for Mauna Loa and Point Barrow (obtained from Keeling at Scripps Institute of Oceanography and from Komhyr at NOAA, Boulder, Colorado) and fossil fuel and cement production data (Rotty 1979) were used. The period of record was 1959-1978. Two graphs were constructed with this information: monthly rate of change of CO_2 concentration in the atmosphere and the annual rate of CO_2 release and uptake at Mauna Loa. To obtain the monthly rate of CO_2 uptake or release we subtracted the mean monthly concentration of CO_2 at month m from the mean monthly CO_2 concentration at month m+1. Assuming that the mean monthly CO_2 concentration occurred in the middle of the month, we then plotted the point at the middle of month m+1. Positive rates of change were plotted below the zero line representing net release of CO_2 (R) and negative rates of change were plotted above the zero line representing net uptake of CO_2 (U). Monthly changes in CO_2 concentration were then assumed to represent the course of uptake (U) or release (R) of CO_2 by plants, animals, and microbes in the terrestrial and marine ecosystems of the Northern Hemisphere. The rate of change curve was then integrated to obtain absolute amounts of CO_2 taken up or released in the hemisphere. The ratio of CO_2 uptake (U) to CO_2 release (R) was then calculated by dividing the integral of the corresponding portion of the rate of change curve.

To produce the graphs of the annual CO_2 uptake and of the annual CO_2 release trends we used the areas above (uptake) and below (release) the zero line respectively of the monthly rate of change curves. The annual anthropogenic CO_2 input from burning of fossil fuel and cement manufacturing was then subtracted from each of the two annual curves to produce corrected annual CO_2 uptake and release curves. The correction assumed that anthropogenic CO_2 inputs were evenly produced through the year. However, since the CO_2 uptake time interval was shorter (5 mo) than the time interval of CO_2 release (7 mo) the correction was greater for the rate of release curve. The corrected CO_2 uptake and release curves were taken as representative of the biospheric metabolic activity. The annual secular increase in CO_2 was calculated by subtracting the CO_2 concentration measured in January of year n from the CO_2 concentration measured in January of year n+1.

We did not subtract the CO_2 input due to burning of natural vegetation resulting from such activities as shifting cultivation and wild forest fires because controversy as to the magnitude of this flux still exists. Calculations of the net input from such burnings range from 1.5×10^{15} gC/yr (Wong 1978) to $\pm 2 \times 10^{15}$ gC/yr (Seiler and Crutzen 1980). However, in response to criticism by Fahnestock (1979), Wong (1979) recalculated his estimate of net CO_2 input to the atmosphere due to burning of vegetation and produced a significantly lower value of 0.6×10^{15} gC/yr.

The concentration of CO_2, measured in units of ppm, were converted to g carbon using the method of Verniani (1966) which is based on the following equation:

$$\text{Mass of the constituent gas} = (\text{mass of atmosphere} - \text{mass of water vapor})\ \frac{VM}{M_a}$$

where: V = volume % of gas in dry air

M = molecular weight of gas = 12 gC/mole CO_2

M_a = molecular weight of dry air = 29 g/mole

Using the above equation 1 ppm of CO_2 is equivalent to 2.118×10^{15}gC.

Results and Discussion

The northern hemisphere exhibits a heterotrophic behavior (U/R=0.86) if anthropogenic inputs of CO_2 are not subtracted from the annual rate of uptake and release curves (Fig. 1). Only during 1960 and 1962 did U=R. The reverse is the case if the anthropogenic CO_2 contribution is deducted from the CO_2 uptake and release curves. For the period of record, U was higher than R with the exception of 1959 when R was slightly higher than U and 1969 when they were almost equal. The U/R varied between 1.0 and 1.4 and averaged 1.2 (SE = 0.02, n = 20; Fig. 1). These results are different from those reported by Hall et al. (1975) using data for the same station for the period of 1959-1972. They found an U/R of about 1 but less than 1 in at least three occasions. The difference in values is due to their correction for oceanic uptake, and in the method of calculating U and R on a seasonal rather than on a monthly basis.

The peak rate of CO_2 uptake occured consistently during August rising sharply after May and decreasing equally fast by September or October. Thus, the length of the growing season was 4 to 5 months (Fig. 2). Release of CO_2 exhibited two maxima, during November and April (Fig. 2).

The monthly rate of CO_2 uptake and release in Mauna Loa are compared with those at Point Barrow in Fig. 3 and Table 1 for the period of record for which there are comparable data. The timing of peak U and R, the length of time for which either process prevails, and the amplitude of change are different from each other. The Mauna Loa station exhibits lower peak rates of U and R, the peak rates of U and R occur later, and the period of U is longer while the period of R is shorter. At Point Barrow, the peak rate of CO_2 uptake generally occurs in July, a month earlier than at Mauna Loa, and the peak rate of CO_2 release occurs in October or November.

Assuming that these data do reflect hemispheric metabolism, the following observations follow:

- hemispheric metabolism appears to be very steady over time and there is little variation in the rates that have been measured;

- in all years the magnitude of U exceeds R but the duration of U is shorter than of R;

- the data do not reflect any serious impact by deforestation or other alteration of the habitat by humans during the last 20 years, nor do they reflect variations that could be attributed to changes in any environmental factor;

- the magnitude of net ecosystem uptake (U) appears to increase and duration of net ecosystem uptake (U) decrease with increasing latitude.

Most authors have assumed that the seasonal variations in atmospheric CO_2 concentration are due to ecosystem activity (Bolin and Bischof 1970, Hall et al. 1975, Junge and Czeplak 1968, Keeling et al. 1976a and b, Lowe et al. 1979, Machta et al. 1977, Pales and Keeling 1965, and Woodwell et al. 1973).

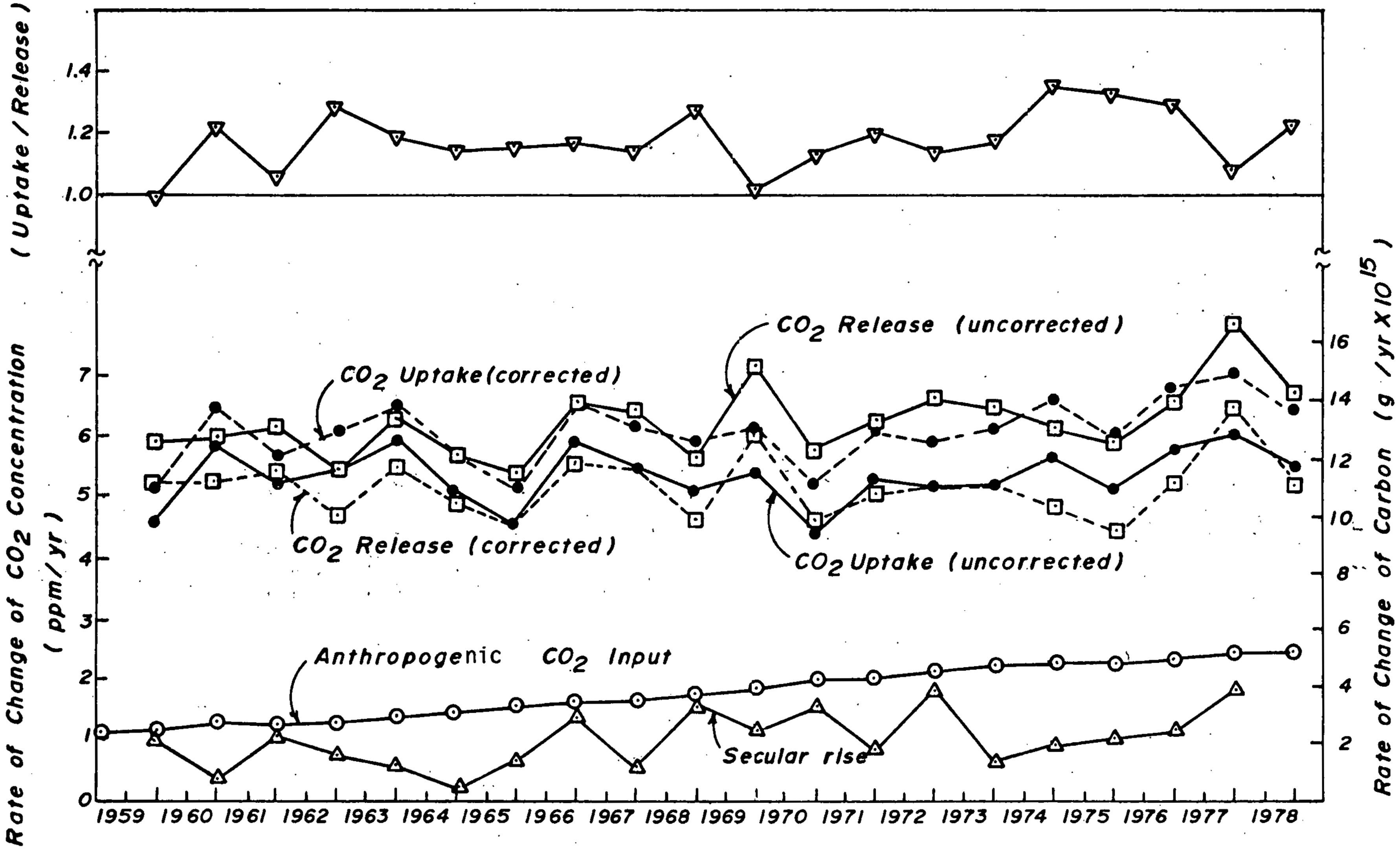

Fig. 1. Annual fluxes of atmospheric carbon dioxide at Mauna Loa. See text for details.

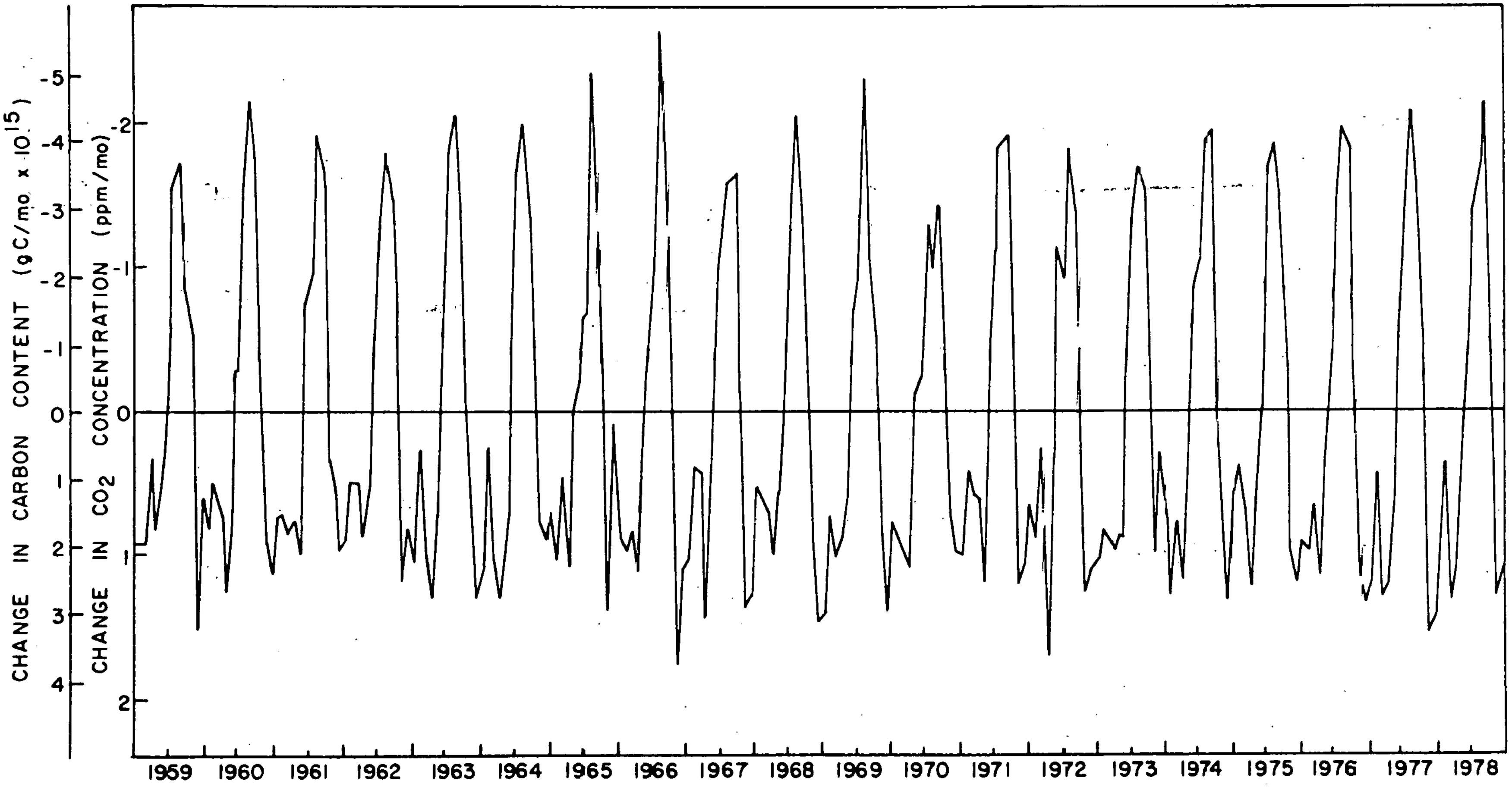

Fig. 2. Hemispheric metabolism as estimated from monthly rate of change of atmospheric CO_2 concentration at Mauna Loa for the period 1959-1978. Net CO_2 uptake (U) is shown above the zero line and net CO_2 release (R) is shown below the zero line.

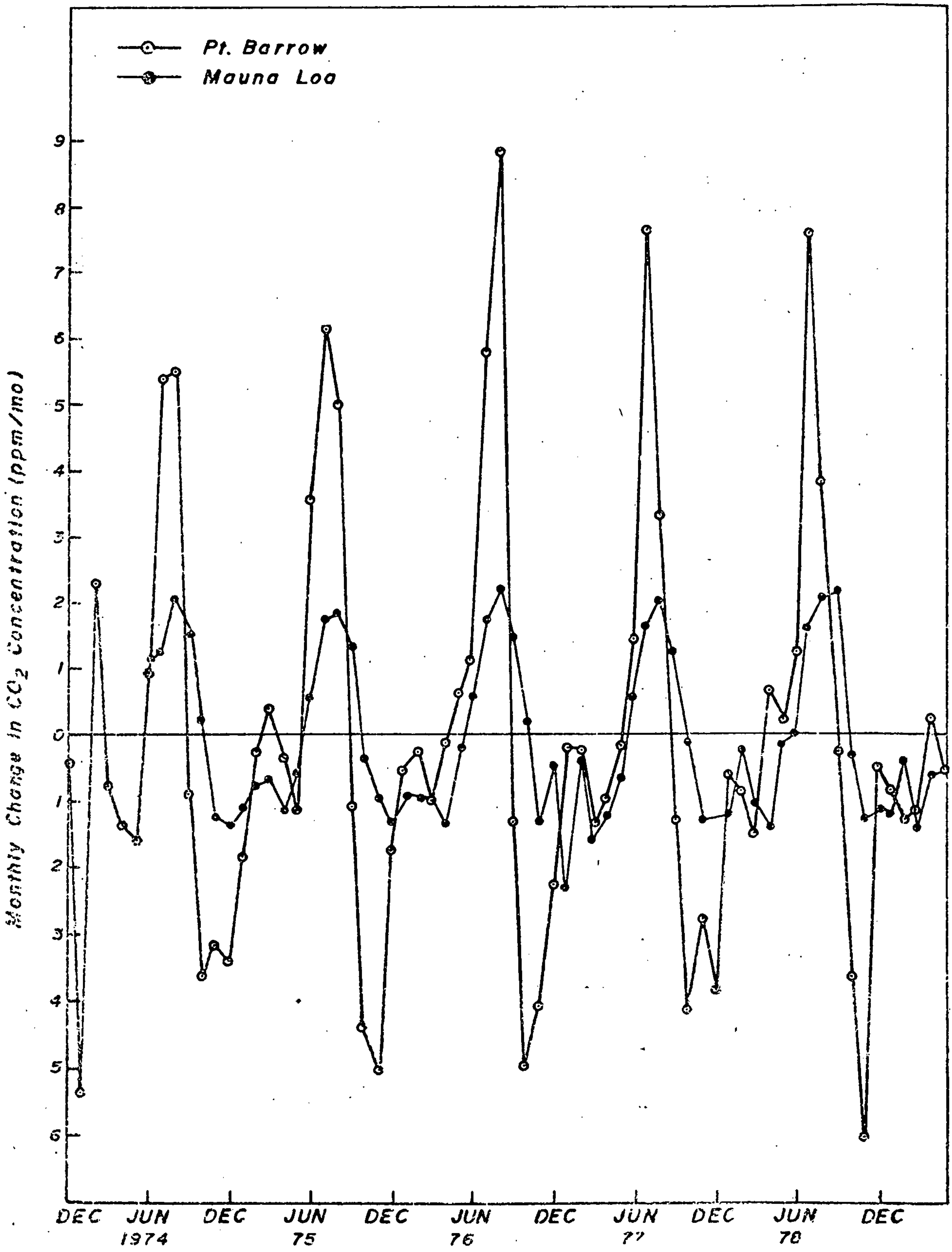

Fig. 3. Monthly rate of change of atmospheric CO_2 concentration at Point Barrow and Mauna Loa monitoring stations for the period 1974-79. These curves are similar to those described in Fig. 2.

Table 1. Mean annual carbon dioxide uptake and uncorrected release rates for Mauna Loa and Pt. Barrow. 1 S.E. is given in parenthesis.

	Mauna Loa (1959-1977)	Pt. Barrow (1974-1978)
CO_2 release (ppm/yr)	6.25 (0.14)	12.07 (1.06)
CO_2 uptake (ppm/yr)	5.36 (0.11)	10.55 (0.36)
U/R	0.86	0.87

However, the reasoning involved in this assumption is not always clear. For example, Machta et al. (1977) used net above ground biomass production data to show that seasonal changes in atmospheric CO_2 did indeed correspond with the changes expected to occur by the productivity of terrestrial ecosystems. However, this calculation is not ecologically sound because atmospheric data reflects net ecosystem metabolism (Hall et al. 1975, Woodwell et al. 1973). By ignoring ecosystem respiration and using net above ground biomass production data, calculations considerably inflate the role of terrestrial uptake of CO_2. Lowe et al. (1979) and Woodwell et al. (1973) confused CO_2 concentration with the rate of CO_2 uptake and release. Thus they incorrectly match peak atmospheric CO_2 concentrations with peak ecosystem activity. The confusion can be clarified with data from the Brookhaven Oak-Pine Forest for which we have the best available ecosystem gas exchange records.

Hall et al. (1975) developed a model of terrestrial biospheric metabolism extrapolated from the behavior of the Brookhaven Oak-Pine Forest. Their analysis shows peak rates of CO_2 uptake during June and peak rates of CO_2 release in December. The atmospheric CO_2 concentration data presented by Woodwell et al. (1973), however, show that the lowest CO_2 concentrations occured in September and the highest in December-January. Woodwell et al. (1973) commented that the largest decrease in CO_2 concentration occured "in the fall as photosynthesis in the northern hemisphere stores carbon". By calculating the rate of change from their Fig. 4, however, one finds that the peak rate of CO_2 uptake occured earlier in the year (June-July as suggested by Hall et al. 1975) rather than in the fall as interpreted by Woodwell et al. (1973). Similarly, peak rate of CO_2 release occured between September and October. In this paper we are basing arguments on rate of change curves not on concentration curves.

Data from the same forest summarized in Botkin et al. (1970) and in Woodwell and Botkin (1970) show that the net primary production of plants remained high between June and September and peaked in July; stem respiration remained high between June and September. Both are out of phase with the atmospheric CO_2 measurements of Woodwell et al. (1973). If we accept that atmospheric changes in CO_2 concentrations as measured at Mauna Loa are indicative of net ecosystem metabolism (Fig. 2), it follows from available data (Table 2) that individual ecosystem compartments are out of phase with the metabolism of the whole ecosystem. If this is true, the suggestion by Lowe et al. (1979) that oceans could be the hemispheric sinks of CO_2 because the timing of plant growth did not match the timing of the late-fall trough of atmospheric CO_2 concentrations, is faulty because he is confusing rates of metabolism with concentration of CO_2 and he is assuming that plant growth is in phase with net ecosystem uptake which is shown not to be the case for the Brookhaven forest. Thus his argument cannot be used to support oceanic waters as hemispheric sinks of carbon.

There is not enough information on net ecosystem metabolism to resolve the question of the timing of peak metabolic activity of the biosphere as reflected by atmospheric CO_2 measurements. It is not clear from the few data for ecosystem compartments whether the metabolism of the whole ecosystem is or is not in phase with the behavior of its components (eg. plants or soil). Table 2 identifies periods of peak metabolic activity in compartments of northern hemisphere ecosystems as reflected in CO_2 exchange measurements. There is no clear relationship with the peak metabolic rates of the hemisphere (Fig. 3). This discrepancy appears to be more significant during the winter

Table 2. Peak metabolic activity of ecosystem compartments and whole ecosystems in the northern hemisphere.

Ecosystem	Compartment	Peak Net CO_2 Uptake (Month)	Peak Net CO_2 Release (Month)	Reference
Brookhaven Oak-Pine Forest	Stems	-	June-September	Woodwell and Botkin 1970
	Producers	July	-	
	Whole ecosystem	June-July	September-October	Woodwell et al. 1973.
Deciduous Forest	Soil	-	August	Edwards 1975
Various Temperate Forests	Soil	-	June-July	Reiners 1968
Florida Fresh-water Marshes	Whole ecosystem	May	May	Lugo et al. 1980
Florida Cypress Swamps	Whole ecosystem	August	-	Cowles 1976; Flohrschutz et al. 1980
Florida Mangroves	Leaf production	August	-	Pool et al. 1975
Subtropical Dry Forest in Puerto Rico	Producers	September-November	-	Lugo et al. 1978
Subtropical Wet Forest	Canopy leaves	March-June	-	Odum 1970

peak of biospheric respiration. It may be that what limits our understanding of this issue is knowledge of the coupling between ecosystems and the atmosphere.

Holdridge (this volume) suggested an alternative hypothesis to explain the Mauna Loa data which, if true, invalidates the previous analysis. He suggested that the seasonal variations in atmospheric CO_2 concentrations reflected the annual variations in the temperature of the atmosphere and the corresponding expansion or contraction of the atmosphere. Yet, measurements at Mauna Loa and Point Barrow are corrected for local temperature and pressure induced changes in CO_2 concentration by continuously comparing air samples with standard gases exposed to the same local atmospheric pressure as the sample gas.

If one accepts the analysis as we have done it in Figs. 1-3, the airshed of Point Barrow appears to be much more productive than that of Mauna Loa in spite of the fact that the Mauna Loa station is reflecting ecosystems at lower latitudes that are known to be more productive than the northern ecosystem (Fig. 3, Table 1). This discrepancy was explained by Keeling et al. (1976b) by the large land areas of forests and grasslands in the higher latitudes relative to the lower latitudes of the Northern Hemisphere. However, there is still much to be learned about atmospheric mixing and where the air at Point Barrow originates and about the role of sea ice in the northern latitudes and their effects on patterns of atmospheric CO_2 concentrations (Ekdahl, personal communication). Atmospheric CO_2 concentration data from the South Pole, where temperature amplitude is also large, do not reflect such an amplitude of metabolism as is observed in Point Barrow. The lower amplitude at the South Pole is explained on the basis of three possibilities: attenuated oscillation from the northern hemisphere, lower terrestrial production, and/or oceanic influences (Lowe et al. 1979). The explanation as to why northern ecosystems would appear to be more productive than southern ecosystems when data from Point Barrow are compared to data from Mauna Loa is not clear and this could in itself invalidate the use of atmospheric data to estimate hemispheric metabolism.

Yet, the most troublesome ecological question raised by the analysis of the Mauna Loa data is the fact that the "apparent" hemispheric metabolism remains so constant over the period of record. In reality, the data reflect an <u>increase</u> in hemispheric CO_2 uptake as can be deduced from the following analogy. In gas exchange measurements of plants, the soil must be isolated because its CO_2 production masks plant CO_2 uptake. If the CO_2 uptake of two identical plants is measured but the soil is isolated in one and not in the other, it would appear that the plant with the soil exposed was taking up CO_2 at a lower rate than the one with the isolated soil. In reality both plants took the same amount of CO_2. At the global scale, anthropogenic production of CO_2 is analogous to the production of CO_2 by the soil and biospheric CO_2 uptake is analogous to plant CO_2 uptake. Figure 1 shows that the rate of anthropogenic CO_2 release has increased from slightly over 1 ppm/year to about 2.5 ppm/year or over 150% in 20 years. In spite of this increase, the "apparent" rate of CO_2 uptake by the hemisphere has remained relatively constant even though the current rate of anthropogenic CO_2 addition is of the order of 50% of the rate of hemispheric CO_2 uptake. If the seasonal change in CO_2 concentration measured at Mauna Loa was regulated by the biota rather than physical forces as suggested by Holdridge (this volume), one would expect that in accordance with the plant-soil analogy, "apparent" hemispheric CO_2 uptake should have decreased in proportion to the rate of anthropogenic input of CO_2. The fact that it did not, implies one or more of the following:

1. The biosphere is responding to CO_2 enrichment by increasing its net carbon uptake.
2. Holdridge is correct in his assertion that the seasonal amplitudes of CO_2 concentrations are artifacts of measurement caused by atmospheric temperature changes.
3. The Mauna Loa data does not reflect the attributed biospheric processes.

With regard to the first implication it appears improbable that the biosphere can respond so fast and to such a degree (20% increase in 1979 alone) to CO_2 enrichment. If the first implication is incorrect and third implication is correct, one must then disregard a significant portion of the ecological analysis of this paper. However, even if Holdridge is correct, it is still possible that part of the seasonal variation is due to biotic factors and that the biosphere is a sink of CO_2. These possibilities are not incompatible with the Holdridge effect. For example, if the seasonal pulses at Mauna Loa were under the control of physical forces only, why do we get a U/R ratio greater than one?

The present analysis of Mauna Loa data can be used to calculate a balance of the movement of CO_2 through the biosphere using a different approach than used before by physical scientists. The balance is based on the integration of rates of change curves (Fig. 2) and is summarized in Table 3. The amount of anthropogenic CO_2 taken up by the biosphere is 50% which is within the range of 44-52% recently quoted by Broecker et al. (1979). Results of ocean uptake modeling indicate that 37% of the fossil fuel CO_2 generated since 1958 to the present has been taken up by the sea (Broecker et al. 1979). If Broecker et al. are right, the remaining anthropogenic CO_2 input (about 13%) have probably been stored in the terrestrial compartment of the biosphere.

The analysis of atmospheric CO_2 data, if correct (sensu Holdridge), conveys the concept of a system that functions as a CO_2 sink at a steady pace in spite of the apparent stressors introduced by humans. For example, if the earth is being deforested as has been suggested (Woodwell et al. 1978) why is the U/R still greater than 1? Perhaps the rate of deforestation is not occurring as fast as suggested. Is it possible that humans are simply creating successional landscapes by stimulating the growth of secondary forests and eutrophic oceans and these systems in turn sequester the carbon products of human activity? Or is the role of the biosphere as a sink masked by forces other than biotic?

Table 3. Carbon balance of atmosphere using Mauna Loa data from 1959-1977.

		Mean	1 S. E.
(a)	CO_2 release (ppm/yr)	6.25	0.14
(b)	Anthropogenic input[a] (ppm/yr)	1.84	0.10
(c)	Corrected CO_2 release(ppm/yr)	4.45	0.12
(d)	CO_2 uptake (ppm/yr)	5.36	0.11
(e)	CO_2 uptake - CO_2 release (ppm/yr) (d)- (c)	0.92	0.11
(f)	Secular rise (ppm/yr)	1.01	0.11
(g)	Uptake-release (gCx10^{15}/yr)	1.94	0.23
(h)	Secular rise (gCx10^{15}/yr)	2.15	0.24
(i)	Anthropogenic input (gCx10^{15}/yr)	3.83	0.21
(j)	(Uptake-release) + secular rise (g)+(h)	4.09	
(k)	% taken up by biosphere (g)/(i)	50%	

[a] Rotty 1979

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LIFE ZONES, LAND-USE, AND FOREST VEGETATION IN THE TROPICAL AND SUBTROPICAL REGIONS

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The probability that terrestrial vegetation may constitute a sink or a gateway to a sink for significant amounts of atmospheric carbon (Holdridge, this volume), must heighten our need for a far more accurate and detailed assessment of biomass, net primary productivity, litterfall, soil organic matter, and the like in terrestrial ecosystems and, more especially, as these relate to the major variables of the natural and human-cultural environment.

In San José, Costa Rica, we have been looking at this problem primarily from the ecological side. By ecological, I do not refer to the specific on-site vegetational and organic matter conditions for, while these are obviously the focus of interest, a great deal more is already known about them than is known or has been recorded for the environmental circumstances upon which they depend. The literature with biomass and productivity assessments for plant communities gives only a most general geographic location. Many studies and reports do provide a cursory statement of regional climate and, perhaps, general terrain conditions, or the biome or plant formation may be named, but it is uncommon to encounter complete and quantified descriptions of all the site factors and land-use conditions upon which the character and actual state of the vegetation, at the time of the biomass and productivity measurements, were ultimately dependent.

As for identification of the plant communities, the situation of classification has been similarly imprecise. Plant communities are named under a variety of general terminologies, some phytosociological, some geographical, some ecological. For none of these are there either quantified criteria or has there been general agreement on distinguishing characteristics except in the most general sense. The classifications are mixed-factorial, combining variable mixes of terms for usually salient features of physical environment and vegetation, as for instance, "evergreen seasonal forest", "tropical rain forest", "dipterocarp-savanna woodland", "dry monsoon forest", "middle taiga forest on podzolic soils", "herbaceous prairie on meadow chernozem-like soils", and others of like ilk with which we are all too familiar. Different authors may employ different terms for the same vegetation or the same term for widely divergent types of ecosystem. Lacking quantified or easily quantifiable criteria and a generic basis, or even general agreement on and employment of a single system of nomenclature, the resultant plot data are difficult to evaluate and compare as "ecosystem-types". This problem is exacerbated by the extreme level of generalization which characterizes these so-called classifications. When we consider how complex and varied the natural environment may be in even a restricted local area and that this complexity may have been enhanced by the effects of past and present human interference, it becomes apparent that the independent variables in these studies have been badly neglected and that this deficiency must be corrected before further field work can yield truly worth-while results.

Two methods for systematic quantified classification of ecosystems (at the climatic level) have existed since the middle of this century. Holdridge's (1967) world Life Zone system of ecological classification was actually published in 1948, the same year as Thornthwaite's excellent modern classification of world climates. Neither system has been applied, until the present, to the requirements for site and vegetational classification in ecosystem productivity and biomass studies, despite the rather obvious advantages for correlation that both possess in this regard.

Life Zone Classification System

The Holdridge classification and methodology is the more ecologically comprehensive of the two; hence it was chosen as a framework for our exercises. Twenty-five years of field trial, projection, and refinement of the original model have now given us a very workable three-level, hierarchial system capable of classifying all terrestrial ecosystems of the earth on a comparative, fully-quantified basis. Moreover, the diagram which models the first-level Life Zone or bioclimatic-vegetational relationship within the system permits correlation, over the whole bioclimatic continuum of the earth with both environmental and vegetational factors for all associations and their successional stages of the natural and cultural vegetation. What this implies, of course, is that the system is predictive. Presuming that values for some points on the chart can be obtained, and that a correlation of some degree does exist with major environmental variables as expressed in the diagram, then unmeasured values may be assigned by interpolation. Similarly, the organization of the model itself facilitates deductions as to the probable types and magnitudes of the correlations to be expected. One of our current approaches in San José is to attempt to correlate existing data on biomass and its components, and on community productivity with Life Zones. I am going to describe the nature and geographic applications of the system itself insofar as these relate to modeling on a regional and world basis.

The first-hierarchial or Life Zone level (Fig. 1) of the classification establishes a quantitative relationship between the principal climatic variables and the major physiognomic features of the associated natural vegetation. The relationship is expressed in terms of equally-weighted ecological divisions of the world's climatic continuum, called Life Zones, which appear on the model diagramming the theory as a series of hexagons set off by logarithmically scaled guide-lines for specific quantitative ranges of long-term average annual biotemperature, precipitation, and effective humidity within what is termed the climatic association. Within the limits for these variables as indicated by its hexagon borders, each Life Zone defines a distinctive set of possible ecosystems, termed <u>associations</u>, which are unique to the given climate.

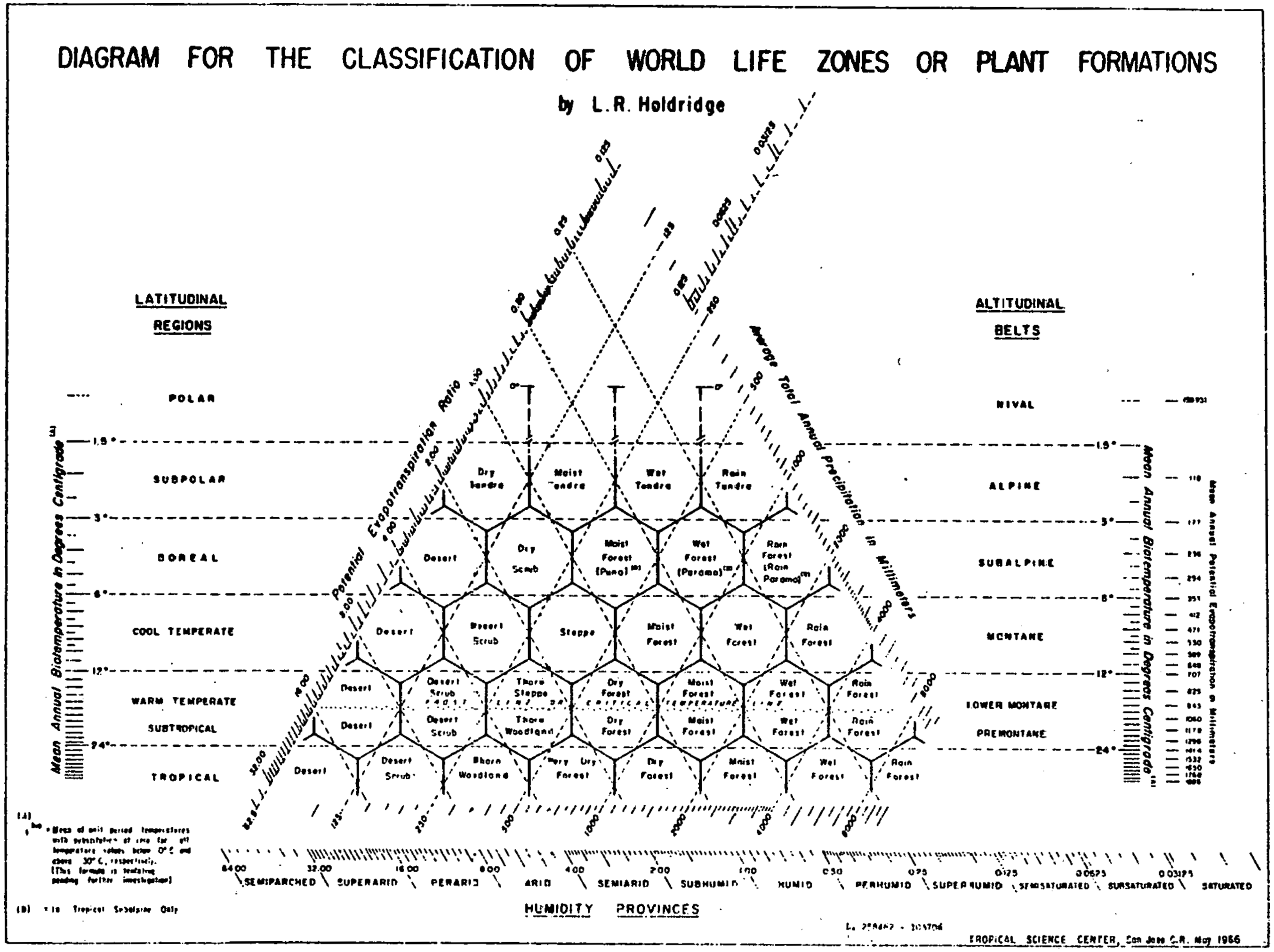

Fig. 1. The Holdridge Life Zone diagram for classifying world plant formations.

The association, as the second-hierarchial level in the system, is defined as an area of land which, under undisturbed natural conditions, supports a distinctive community of living organisms, evolved for adaptation to a specific narrow range of atmospheric, edaphic, and hydrological conditions. An association is identified, ideally, from the physiognomy of its mature, evolved, natural vegetation, but in the absence thereof, successional stage vegetation or even edaphic and other site factors may be used instead. Because the same combination of physical conditions may recur worldwide, associations are not defined or described in terms of the floristic dominants. Obviously, the taxa will differ from one biogeographical region to another. The actual number, character, and landscape arrangement of the associations within any area of a given Life Zone will be determined by the particular combinations of geological substrate, landform, special atmospheric conditions including exposure, drainage, and soils which exist there, but all of these features except bedrock geology will bear the stamp of the bioclimatic itself. By definition, no association may occur in more than one Life Zone.

While the association is a relatively stable unit as a site, local variability in biomass and productivity may be introduced by long and short-term changes in the vegetational cover and associated soil and biota due to terrain evolution, natural disturbance, and the disturbances resulting from hunting, burning, cultivation, grazing, timber-cutting, and other human land-using activities. Recognition of the successional stages of each single association, which is accomplished at the third or most-detailed level of the classification, is of special importance because land management activities deal primarily with the manipulation and control of natural successional processes. Each association will have a distinctive set of successional stages, rates, and components under natural conditions and will react differently to manipulation and control of both natural and artificially-imposed vegetations. In the evaluation of vegetation for biomass and productivity values therefore, it is important to ascertain not only the Life Zone and association with which one is dealing, but also the successional stage in its relation to the mature, natural climax state towards which succession is proceeding. From failure to meet this requirement, the data from much past research may have been incorrectly interpreted in terms of regional or world-wide estimates of biomass and productivity.

While any land station in the world can be readily classified to Life Zone from simple climatic data, the greater value of the system is that it permits precise identification and detailed field mapping of Life Zone distributions directly from observations of the natural mature and second-growth vegetation, and also, from cultivated vegetation and of the terrain in which it occurs. Viewed as a total landscape, the physiognomy and life forms of this vegetation will be distinctive for each Life Zone. Long-experienced observers are capable of distinguishing even the specific transition zones which are represented by the triangular areas between the guidelines and the hexagon boundaries on the chart. This capability is made more objective by the development of indices relating measured aspects of forest and woodland physiognomy to Life Zone and association (Holdridge 1962, 1967). These indices and formulas as well as detailed descriptions of vegetation and soils as correlated with the Life Zone system (in the tropics and subtropics principally), provided increasingly accurate bases for the methodology. They make the system especially valuable for both climatic mapping and ecological site classification in the less-developed regions where reliable, long-term meteorological station-data networks are usually sparse or non-existent over extensive land areas. Many still-forested areas of the world, tropical and otherwise, fall into this latter category.

Worldwide, more than 120 different Life Zones may be recognized. However, the diagram sets no absolute limit, as we have encountered bioclimates which fall well outside the climatic limits of those given names both on the dry and the wet sides of the chart (Fig. 1). Of the more common Life Zones, however, the greater number are found in low latitudes where, near sea-level, frost or critically low temperatures do not occur. These "tropical" bioclimates are distributed between two latitudinal regions (repeated in each equatorial hemisphere): the Tropical region with roughly 38 Life Zones in seven altitudinal belts and eight humidity provinces and the Subtropical region with 30 Life Zones in six altitudinal belts and seven humidity provinces. These two regions account for almost 60 percent of all Life Zones and together comprise what is commonly termed the "tropics" in other systems and nomenclatures. However, they are significantly different as regions and the Subtropical region is, except for the absence of cold-tolerant plant species, in closer affinity to the Warm Temperate region, with which it shares a belt of hexagons, than with the Tropical region. Failure to have made this distinction has been a continuing source of difficulty in assigning ecologically meaningful geographic limits to the tropics in vegetational and climatic studies. In some of the literature, including a recent publication by Rodin, Basilevich and Rosov (1975), the Warm Temperate region of Holdridge's system is actually termed "subtropical". This is equivalent to taking the subtropics to the latitude of New York City, but may be consistent with Russian perception of "tropical" climates. By way of comparison, for the "tropics" are commonly believed to be climatically the least complex, the Warm Temperate region includes 23, the Cool Temperate region 16, and the Boreal region only 9 Life Zones. Life Zone maps reveal not only a greater number and range of bioclimatic types in the tropics and subtropics,but also a greater degree of both aggregate and localized climatic diversity. In Peru, a recent updating of an early reconnaissance-level map reveals the presence of 71 Life Zones in two regions alone. Such an extreme range of bioclimates is due in part to the vast north-south trending Andean mountain system, with its marked relief, topographic, and orographic contrasts. Field mapping indicated that the Amazonian "rainforest", which covers almost two-thirds of the Peruvian territory, is climatically diverse as well, with some 12 Tropical region and six Subtropical region Life Zones being identified, in locally complicated patterns, from the forested eastern slopes of the Andes to the country's northern and eastern frontiers. Similarly, a provisional map of Nigeria (Tosi 1968) based upon data from meteorological stations alone, shows that within the former colonial limits of that country there are a total of 17 Life Zones, two of which fall into the Subtropical region and the remainder in the Tropical.

The pronounced diversity of bioclimates in Tropical and Subtropical regions is well-illustrated by tiny Costa Rica and Panama, each with 12 Life Zones distributed in locally intricate geographical patterns. Holland, by comparison, has only one Life Zone and in the entire conterminous United States east of the 102 meridian, only 10 have been mapped. The characteristically more-uniform climatic pattern of the mid-and high-latitudes is the product of predominantly frontal weather along broadly oscillating air-mass boundaries. A single major Life Zone may, as a result, extend unbroken over hundreds of miles, being interrupted by others only when major relief features lower temperature at higher elevations. In the lower latitudes, however, frontal-type weather is uncommon or absent, being replaced by wet seasonal convectional dynamics and dry season orography as the principal mechanisms of precipitation. Recent studies of tropical Life Zone distribution indicate that even where relief is subdued, as over extensive lowland plains and upland plateaus, modest local increases in the general elevation will be accompanied by markedly increased precipitation and cloudiness. The result is an often striking degree of localized climatic variation. This reaches an extreme, of course, in mountainous areas where one bioclimate replaces another in banded series of narrow strips some less than 1 km in width. Orographic "rain shadow" effects due to the advective transport of the latent heat of condensation are often so pronounced that cool, highly humid, wet and rain forest Life Zones on one exposure give way to hot, dry thorn woodlands and desert bush Life Zones a scant few kilometers away. On the extensive plains and plateaus, these effects are moderated but not eliminated. Given the bias in locating weather stations in the relatively drier valleys and riverside areas where human settlements are concentrated, this complexity has gone largely unnoticed by climatologists and is not represented on conventional precipitation maps. Average rainfall conditions over extended areas in the tropics have, as a consequence, been badly underestimated on such maps.

Given the diversity and wide range of bioclimatic conditions now discerned in the lower latitudes, to which we must add the localized complexity resulting from differences in landform position, soils, drainage and the like, it stands to reason that there will be equally great vegetational diversity under undisturbed natural conditions. Because each Life Zone and association within a Life Zone area is distinctive as an environment, human development of landscape will be equally diverse and will have followed a different historical pattern. So it is logical to conclude that few generalizations can be made as to biomass and productivity in these two great latitudinal regions. Yet, a considerable number have been made. However, very little of the tropical environment has been subjected as yet to sound, comparative study of its component vegetational communities. That is a task which awaits us.

Land Use in Tropical and Subtropical Regions

The Life Zone System has been applied to the bioclimatic mapping of much of tropical and subtropical Central and South America, except Brazil, to most of the Caribbean Islands except the Lesser Antilles and Cuba, to Mozambique and Timor, to parts of Thailand, and, on a provisional basis from climatic data alone, to Australia, Nigeria, the Mediterranean region, the State of Colorado, and the eastern half of the United States. The "tropics", while receiving the greater part of the more detailed mapping, are still far from completed.

An approach being tested is detailed evaluation of vegetation cover conditions and trends in a few selected tropical and subtropical-region countries for which up-to-date and detailed Life Zone maps are already available. Data for this exercise has proven to be both difficult to obtain and, for many countries, the data has proven to be unreliable in many varying degrees.

As an example, I have summarized the findings for Costa Rica, for which we were able to obtain reliable information.

Table 1 shows the general relationship of Life Zones to total national territory and to domography in the five Central American republics. These data were obtained from the original Life Zone maps and from the 1960-1963 census of population. The Table illustrates the degree to which historical development and population density have been biased towards Life Zones in the subhumid and humid provinces and, among these, towards the cooler elevation belts. Those Life Zones with the very highest population densities in each country reflect urban concentrations which in turn reflect historical agrarian settlement tendencies. In Costa Rica and El Salvador there are marked urban concentrations in the Premontane (P-mf) and Subtropical Moist Forest (S-mf) Life Zones which contain the national capital in each case, and most of the provincial capitals. In Guatemala, the capital is located in the Subtropical Dry Forest (S-df) and the principal provincial cities are all located in the Lower Montane Dry Forest (LM-df) Life Zone. The capital of Honduras is found in an upland valley in the Subtropical Dry Forest but is surrounded by mostly Subtropical Moist Forest in the agricultural areas. Two Life Zones, the Tropical Moist (T-mf) and Subtropical (or Tropical Premontane) Wet Forest (S/P-wf) occupy approximately 54% of the land area in Central America yet they contained only about 10% of the population in the early 1960's.

Not only population,but also the intensity of economic activity in agriculture tend to be strongly concentrated in the Life Zones clustered on either side of the unity line of humidity on the chart (Fig. 1), where mean total annual rainfall is equal to potential evapotranspiration. In these Life Zones, climatic and soil conditions are most favorable to sustained and productive agricultural production; those at higher elevations for temperate grain, dairy, and green vegetable crops for family subsistence; and those at lower, warmer levels for the traditional plantation crops for export, as banana, oil palm, cacao, coffee and, more recently, cotton, rice, and beef cattle.

In Table 2, I have summarized the findings of Langham (1965) from a 1964 sample study of land utilization around the Costa Rican vegetation study sites of Holdridge et al.'s (1971) 1964-1967 work for the U. S. Defense Department. Langham mapped land-use in detail in areas ranging from 4-14 km^2 around each of 11 study plot areas, representing 10 different Life Zones. Humid Life Zones are clearly preferred for cultivation of crops, with low-mid and mid-elevation temperature belts preferred over the hottest lowland belt. Extensive grazing is the predominant use of farmland in the lowland subhumid and humid provinces and intensively-managed pastureland for dairy production occupies most of the farmland in the mid-elevation (Premontane) and high elevation (Lower Montane and Montane) perhumid and superhumid Life Zones. The percentages of pasture in the mid- and upper-elevation belts correspond almost totally to dairy production which requires generally wet and cool areas.

Table 1. Estimated population density and area of Life Zones in five Central American Republics. (Tosi and Voertman 1964).

Life Zone[a]	Guatemala Pop.Density (#/km²)	Guatemala Area (km²)	Honduras Pop.Density (#/km²)	Honduras Area (km²)	Nicaragua Pop.Density (#/km²)	Nicaragua Area (km²)	Costa Rica Pop. Density (#/km²)	Costa Rica Area (km²)	El Salvador Pop.Density (#/km²)	El Salvador Area (km²)
T-vdf	36.8	1.6	38.8	0.3	12.8	2.6	-	-	-	-
LM-df	376.9	0.4	-	-	-	-	-	-	-	-
S-df	71.1	11.7	113.3	1.7	33.3	1.5	-	-	64.0	0.5
T-df	8.8	23.2	34.0	17.2	27.5	22.4	12.7	12.1	101.0	13.7
M-mf	46.1	0.7	-	-	-	-	-	-	-	-
LM-mf	50.5	15.8	17.8	3.0	-	-	238.5	0.1	-	-
S/P-mf	32.3	4.7	22.0	32.7	22.3	9.4	216.2	1.7	246.6	6.6
T-mf	11.0	38.9	5.5	40.6	1.6	57.5	6.2	17.4	-	-
M-wf	14.8	0.1	-	-	-	-	-	-	-	-
LM-wf	17.5	3.2	1.6	2.4	0.6	0.5	21.6	2.0	30.0	0.2
S/P-wf	16.5	8.1	2.7	16.1	1.0	42.4	8.5	11.1	-	-
T-wf	-	-	-	-	3.0	2.0	4.1	2.3	-	-
P-rf	-	0.5	-	-	-	0.3	1.4	4.3	-	-
Average Pop. density	26.1		16.1		7.6		15.7		117.8	
Total Area		108.9		114.1		138.7		51.0		21.4

[a] T = Tropical, S = Subtropical, M = Montane, LM = Lower Montane, P = Premontane, df = Dry Forest, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

Table 2. Area in major land use categories as a percent of all land in Life Zone sample areas (after Langham 1965).

Life Zone[a]	Crop Land	Pasture Land	Forest or Brush	Misc. Land Use
		(%)		
T-df	0.45	40.62	58.83	0.10
P-mf	66.39	19.73	9.73	4.30
T-mf	25.51	45.36	23.73	5.40
T-mf/P-wf	56.77	14.68	19.42	9.13
P-wf	7.58	42.88	45.53	1.01
M-wf	6.84	29.69	61.73	1.74
T-wf	4.18	3.12	90.29	2.41
LM-wf	9.40	35.55	53.13	1.92
P-rf	5.85	29.04	61.26	3.85
M-rf	0.12	4.13	92.19	3.56
LM-rf	0.33	33.64	63.26	2.77

[a] T = Tropical, P = Premontane, M = Montane, LM = Lower Montane, df = Dry Forest, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

At the time of Langham's study, there was appreciably more forested land in all Life Zones of Costa Rica than at present, as we shall see in the following Tables, but Table 2 does illustrate the point that agricultural settlement and concommitant deforestation do not proceed randomly, but are strongly biased to specific environments within even a small tropical country. Therefore, the high temperature, basal belt lowlands from subhumid to perhumid, and wet and rain forest Life Zones of mid-and upper-elevational belts, in that order, are the last to be entered by farmers. In Costa Rica, these retained the highest percentages of forested land in the areas sampled. As we shall see, however, even these areas are today being intervened for economic development.

Forest Vegetation in Costa Rica

Table 3 breaks down forest cover into primary and secondary forest by Life Zone as determined by Langham's (1965) sample. Tropical Montane Rain Forest, Tropical Wet Forest, Tropical Premontane Wet Forest, and Tropical Premontane Rain Forest had the highest percentages of land still in forest and the highest percentages of primary forest in the areas he studied. In the moist and dry forest Life Zones, forested and brush covered land, as a percentage of all land, constituted not only a lower percentage of all land, but a greater proportion of it was in a secondary successional condition as a result of natural regeneration on land abandoned from agricultural or grazing use.

In Table 4 I have compared the best forest cover data for the period 1971-1977 in order to assess the deforestation rate in Costa Rica. The Life Zone areas are taken directly from the updated Life Zone map of the country (Tosi 1969). The forest cover data are from Tosi (1972), based on official agricultural census figures, and from Sylvander (1978), based on aerial photographic interpretation of the vegetational cover in that same year. Life Zones with small total land areas have been grouped. The results indicate an average decrease in the forest area of Costa Rica, amounting to 3%/yr over 6 yr. The Food and Agricultural Organization (FAO) estimated deforestation in Costa Rica as 571.27 km^2/yr over the 15-yr period 1961-1976, for an average of 2.7%/yr, which is a pretty close fit to my estimate. Presumably the annual loss would have been lower in the decade 1960-1970.

What is most interesting in our results however, is the variation in the deforestation rate by Life Zone. Among the Life Zones with a large total area, the Tropical Moist Forest, preferred for cattle ranching and commercial banana cultivation, but principally the former in terms of area utilized, leads all others with 7.6%/yr. The Premontane Wet Forest, which in Costa Rica occupies a large transitional area at fairly low elevation, followed with 3.7%/yr and had the next largest total deforested area. Land clearing for cattle production under extensive ranching systems is the sole basis for deforestation in this wet Life Zone, as is the case with Tropical Wet Forest, third on the list in absolute area but with only 2%/yr deforestation rate. These wet forests are still comparatively inaccessible compared to those of the humid province. In

Table 3. Percent forest cover by Life Zone (adapted from Langham 1965).

Life Zone[a]	Total Forest Cover	Primary Forest	Secondary Forest	Unclassified
		(%)		
T-df	58.8	3.0	4.4	51.4
T-mf	23.7	15.4	8.3	
P-mf	9.6	0.0	9.6	
LM-mf	-	-	-	
T-wf	90.3	66.6	23.7	
P-wf	54.2	44.0	10.2	
LM-wf	53.1	16.7	36.4	
M-rf	92.2	72.3	19.9	
LM-rf	63.3	29.2	25.7	8.4
P-rf	61.3	43.9	17.4	

[a] T = Tropical, P = Premontane, LM = Lower Montane, M = Montane, df = Dry Forest, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

Table 4. Forest cover and estimates of deforestation in Costa Rica.

		Forest Cover[b]					
Life Zone[a]	Total Area	Area 1971		Area 1977		Deforestation	
		(km^2)	(%)	(km^2)	(%)	(km^2/yr)	(%loss/yr)
T-df	3,755	964	25.7	733	19.5	38.5	4.0
T-mf	9,944	3,928	39.5	2,130	21.4	299.7	7.6
P-mf	3,666	944	25.8	647	17.6	49.5	5.2
LM-mf)	124						
LM-wf)	912	3,183	69.4	3,091	67.4	15.3	0.5
LM-rf)	3,548						
T-wf	11,431	7,191	62.9	6,348	55.5	140.5	2.0
P-wf	11,909	5,040	42.3	3,926	33.0	185.7	3.7
M-wf	34						
M-rf	1,143	949	80.6	647	55.0	50.3	5.3
P-wf	4,406	3,210	72.9	3,320	75.4	+18.3	+0.6
TOTALS	50,900	25,409		20,842		761.2	3.0

[a] T = Tropical, P = Premontane, LM = Lower Montane, M = Montane, df = Dry Forest, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

[b] Areas in 1971 are from Tosi (1972) and in 1977 from Sylvander (1978).

Costa Rica, the Tropical Dry Forest is not very extensive and most of its forests were decimated in the decade 1950-1960 following the construction of the Inter-American Highway, but it is still a popular area for land-clearing (4%/yr), now mostly for the conversion of formerly wooded summer grazing lands into open pastures and croplands. With impending large irrigation projects, however, probably all forests in this Life Zone will be terminated in less than 20 yr.

Wet and Rain Forest Life Zones retain the most original forest cover and may continue to do so in topographically broken and steep regions where they are now increasingly protected in National Parks and in Forest Reserves decreed to protect water resources.. If it should turn out that these forests are also those from which soil carbon is leached to groundwater most readily, which would be reasonable to suppose, then there may be international justification to regulate land uses in these Life Zones. The Premontane Rain Forest appears in the data to have gained some forest land in this period. This might result from allocation of area to different Life Zones in the two surveys, but environmental conditions are so severe that little colonization takes place and, in such areas as are entered, there is much subsequent abandonment of fields and pastures to second-growth succession.

Reforestation has only recently become a popular activity of sorts in Costa Rica, being the consequence of conservationist outcries, a free press, and economic interests pressuring the government into enacting a reforestation law granting generous financial inducements to large landowners for each hectare successfully reforested. As can be appreciated from Table 5 and Fig. 2 and 3, the reforestation program is still largely in the planning stage with a large area projected for planting in the future. Prior to 1979, the rate of forest planting was negligible, being estimated at no more than 100 ha/yr. Natural reforestation occurs as the result of land abandonment, but it may be reversed with changing owners.

Timber cutting for lumber and plywood is not the principal cause of deforestation in Costa Rica, nor in most other Central and South American countries. However, it almost always acts as a stimulus to colonizers who invade, clean up, and settle along roads constructed by loggers. The industry is not committed to owning forest land or insuring the future of its raw material supply. Over the last 12 yr an average of eight new sawmills have been installed each year. Table 6 shows the distribution, capacity, and raw material source by Life Zone of the currently existing mills. The majority of these mills are located in the Tropical and Premontane Wet Forests. Tables 7 and 8 show, respectively, the volume of wood entering these mills by Life Zone source and the estimation of the quantity of wood actually utilized from the forests in terms of the forest area actually needed to supply this volume per year. When we compare the area required to provide the annual supply of wood to the sawmills (7,256 ha) with the annual deforestation rate (76,120 ha; Table 4) it becomes apparent that less than one-tenth of the forest removed each year is providing all wood utilized (except some fencing, firewood, and charcoal) including all the wood going into export (25,000 m^3/yr). Logs are not exported. The remainder is left to rot or is burned in land clearing.

Table 5. Annual reforestation, by Life Zones, in Costa Rica during 1979.

Type of Reforestation	Life Zones[a]								TOTAL	
	T-df	P-mf	T-mf	T-wf	P-wf	P-rf	LM-wf	LM-rf	(ha)	(%)
	(ha)									
Artificial	413	125	622	238	487	-	2	-	1,887	23
Natural[b]	756	258	800	1,305	1,445	1,445	142	123	6,150	77
TOTAL	1,169	383	1,422	1,543	1,932	1,321	144	123	8,037	100
%	14	5	17	20	24	16	2	2	100	

[a] T = Tropical, P = Premontane LM = Lower Montane, df = Dry Forest, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

[b] From abandonment of land.

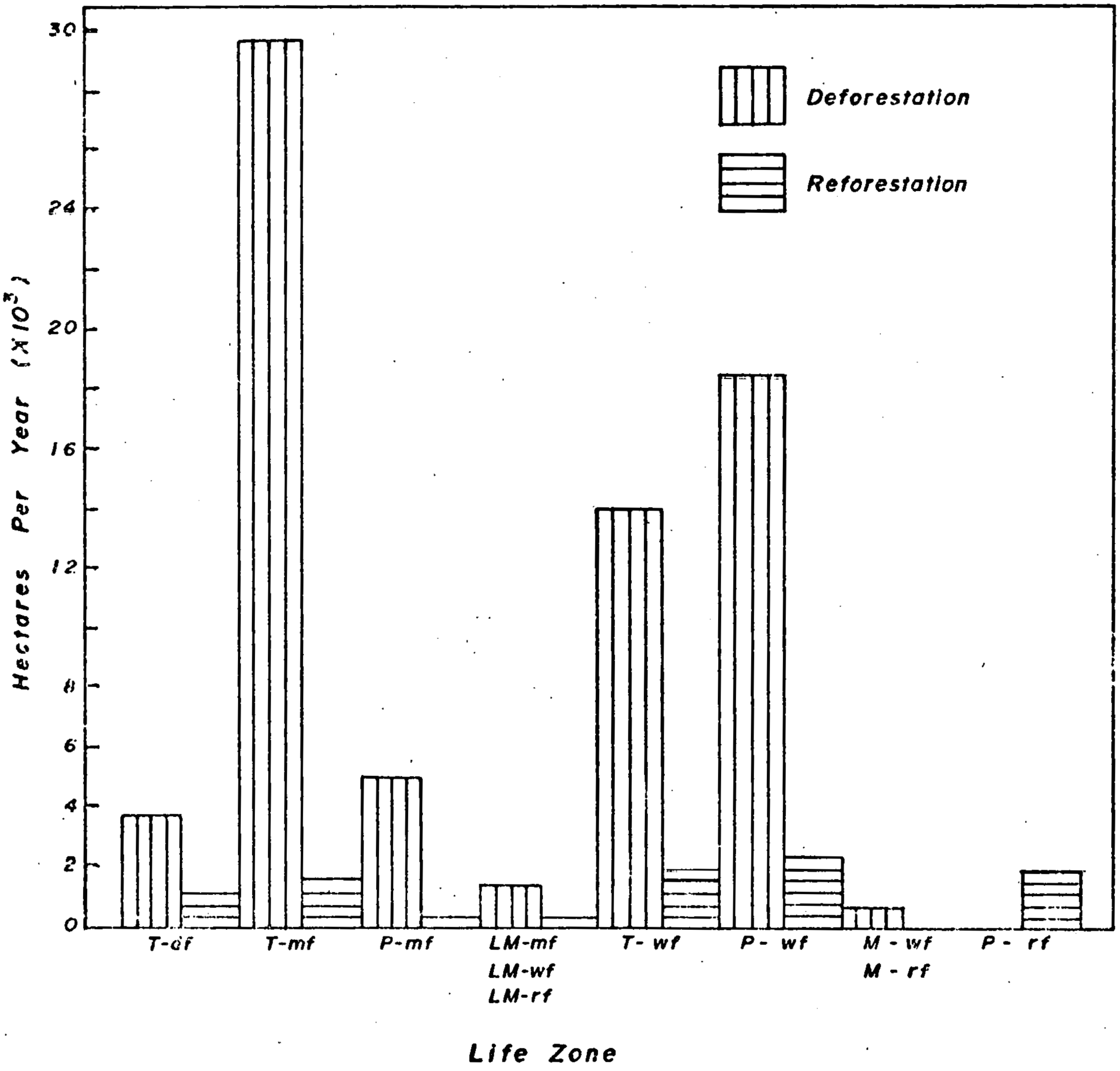

Fig. 2. The rate of deforestation and reforestation in Costa Rica for the period 1971-77.

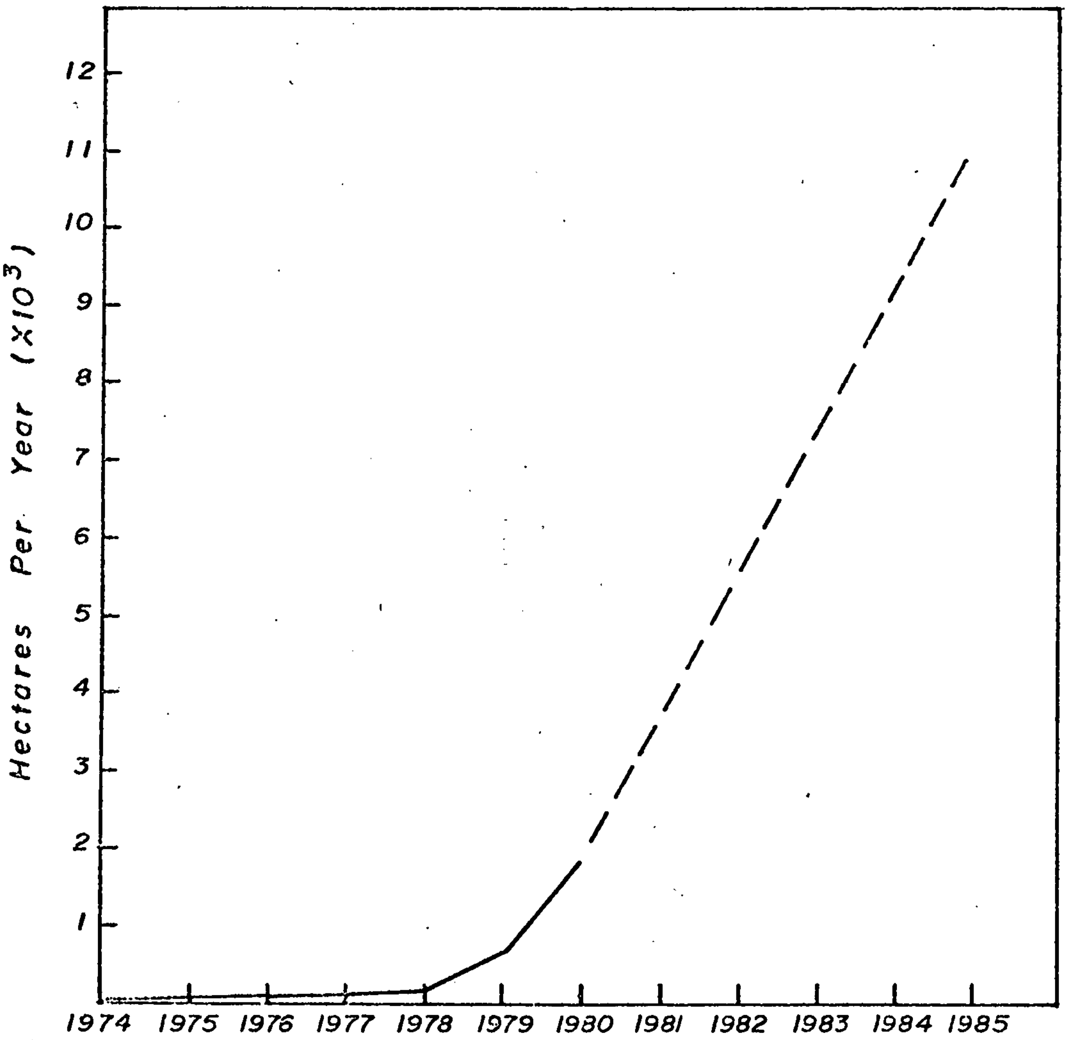

Fig. 3. The rate of artificial reforestation in Costa Rica for the period 1974-79.

Table 6. Distribution of sawmills by types and Life Zones 1979.

Mill Type	Mill Class Range (m^3/day)	Average Capacity of Mill (m^3/day)	Total Mills	Number of Sawmills by Life Zone[a]				
				T-mf	T-wf	P-wf	LM-wf	LM-rf
A_1	+25.1	170	1[b]				0	0
A_2	+25.1	45	20	5	6	9	0	0
B	20.1-25	22.5	16	1	7	8	0	0
C	15.1-20	17.5	10	2	1	6	1	0
D	10.1-15	12.5	43	4	13	21	2	3
E	5.1-10	7.5	27	1	8	16	1	1
F	1-5	2.5	100	9	42	45	0	4
TOTAL			217	22	77	104	4	8

[a] T = Tropical, P = Premontane, LM = Lower Montane, mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

[b] Supplied with wood from three Life Zones, T-mf, T-wf, P-wf.

Table 7. Wood volume entering sawmills.

Mill Type	No. of Mills	Capacity[a] x̄ individual (m³/yr)	Volume of Wood Sawn by Life Zone[b]					Total
			T-mf	T-wf	P-wf	LM-wf	LM-rf	
			(m³/yr)					(m³/yr)
A_1	1	34,680	6,936	13,872	13,872	0	0	34,680
A_2	20	9,180	45,900	55,080	82,620	0	0	183,600
B	16	4,590	4,590	32,130	36,720	-	-	73,440
C	10	3,570	7,140	3,570	21,420	3,570	0	35,700
D	42	2,550	10,200	33,150	51,000	5,100	7,650	107,100
E	27	1,530	1,530	12,240	24,480	1,530	1,530	41,310
F	100	510	4,590	21,420	22,950	-	2,040	51,000
TOTAL	217		80,886	171,462	253,062	10,200	11,220	526,830
%			15	33	48	2	2	100

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[a] It was presumed that mills worked at two-thirds capacity (Forest Service figure) and that there was a 6-day work week, 51 weeks a year.

[b] T = Tropical, P = Premontane, LM = Lower Montane
mf = Moist Forest, wf = Wet Forest, rf = Rain Forest.

Table 8. Total wood harvested for sawmilling and area required for its production by Life Zone.

LIFE ZONE[a]	Harvested Wood (m^3/yr)	Est. Wood Volume Actually Used (m^3/ha)	Area Required to Supply Wood Used (ha)
T-mf	80,886	60	1,348
T-wf	171,462	80	2,143
P-wf	253,062	75	3,374
LM-wf	10,200	50	204
LM-rf	11,220	60	187
TOTAL	526,830	$\bar{x}$ = 65	7,256

[a] T = Tropical, P = Premontane, LM = Lower Montane
mt = Moist Forest, wf = Wet Forest, rf = Rain Forest.

From the foregoing, it is apparent that Costa Rica may be wasting a tremendous opportunity to industrialize on the basis of its forests, presuming correct land-use and intensive management linked to permanent and high-order industry. Failure to do so has stemmed from ignorance of the opportunity, the orientation of its businessmen to rapid turnover of capital for high returns, and to prestige activities such as ranching. The North American market for cheap beef is a major force for deforestation and the consequent lack of modernization in the forest industry. However, this situation could shift rather rapidly and there are some signs now that it may do so, with two new forestry schools, a moratorium on new timber concessions, a reforestation law, and conservationist pressures to stop destruction of forests in high rainfall areas. From a 3%/yr forest area loss, Costa Rica could shift within a few years to the reverse, with whatever limited effects this might have on the world carbon cycle.

We cannot generalize to the tropics as a whole from Costa Rica. Each country is sufficiently different to warrant a separate analysis, but these analyses will also require that we relate forest covers to Life Zones if we hope to get a correct appraisal of the real situation.

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PRELIMINARY ESTIMATE OF THE STORAGE OF ORGANIC CARBON IN TROPICAL FOREST ECOSYSTEMS

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Introduction

The tropics contain about 50% of the world's forests (Unesco 1978) and according to most reviews (e.g. Olson et al. 1978, Rodin and Bazilevich 1967, Whittaker and Likens 1973), tropical forests store more organic matter per unit area than most temperate or boreal forests. Estimates of total organic matter storage in tropical forests suggest that they are extremely important as potential sources or sinks of carbon in the biosphere. Given the many questions that are still unanswered about the carbon budget of the biosphere (e.g. Olson et al. 1978) it is imperative to have a better understanding of the role of tropical forests in the carbon balance of the world. A pivotal piece of information in most calculations of this role is the amount of organic carbon stored in these forests. Using organic carbon storage figures scientists calculate potential rates of release of CO_2 after burning or deforestation (Wong 1978, Woodwell et al. 1978), rates of organic carbon turnover (Olson et al. 1978) or rates of organic carbon accumulation (Broecker et al. 1979).

The most often quoted estimate of organic carbon storage in tropical forest ecosystems is the one by Whittaker and Likens (1973). These authors estimated the amount of organic carbon stored in these forests by first estimating the area of forest lands using world maps and a number of miscellaneous sources of information including FAO world forest statistics. They then multiplied these forest areas by estimates of plant biomass derived mostly from Lieth (1975), Rodin and Basilevich (1967), and a number of other sources, none of which was an original source. An analysis of the four literature sources used by Whittaker and Likens to estimate organic carbon storage in tropical ecosystems reveals that their summaries are based on a minimum of 13 original sources some of which report root biomass but most report only above ground biomass. They grouped tropical forests in two categories: tropical rain forests and seasonal forests.

A less quoted attempt to estimate the organic carbon storage in tropical forest ecosystems is that of Olson et al. (1978) who used similar sources of information as Whittaker and Likens but divided tropical forests into six categories rather than two. Olson et al. (1978) differentiated between moist, wet, dry, and montane forests. For the calculation of organic carbon storage they added "dead organic matter" to "live" organic matter storage. Olson et al. (1978) arrived at lower estimates of tropical forest areas and lower estimates of organic carbon storage than Whittaker and Likens (1973).

A more recent estimate (Ajtay et al. 1979), of the organic carbon storage in tropical forests used the same two categories as Whittaker and Likens (1973) but added mangroves as a third category. Their sources of information for plant biomass were similar to those of Whittaker and Likens with adjustments in light of more recent data derived mainly from IBP studies. The estimated areas of tropical forests used by Ajtay et al. were considerably lower than those used by Olson et al. (1978) and by Whittaker and Likens (1973). They arrived at an estimate of organic carbon storage in tropical forests that was lower than either Olson et al's. or Whittaker and Liken's estimates.

In this paper we have examined about 41 original sources of information dealing with plant, litter, and soil organic matter or organic carbon storage in tropical forest ecosystems in an attempt to improve the estimates given by Ajtay et al. (1979), Olson et al. (1978) and by Whittaker and Likens (1973).

Approach

We used the Life Zone system of Holdridge (1967) as the conceptual framework on which to base estimates of organic carbon storage in tropical ecosystems. The fact underlying this approach is that tropical forest environments are more diverse than temperate or boreal forest environments and that each type of forest environment has an intrinsically different capacity to produce organic matter. For example, of the approximate 120 Life Zones in the world, 68 are tropical (Fig. 1). The complexity and organic matter production of vegetation varies with Life Zones and generally increases towards the wet tropical Life Zones (Holdridge 1967). Thus, the role of tropical forests relative to the carbon budget of the earth must be weighted according to the relative area of and organic carbon storage in the various tropical Life Zones. The Life Zone concept is used because it has universal applicability, it is based on quantitative climatic relationships using information that is normally available for most parts of the world, it is an objective method for classifying environments, it has been used extensively worldwide, 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 production information is not available. Our approach consisted of the following steps:

- definition of the tropics;
- summary of the world estimates of land and forest areas in tropical countries;
- classification of tropical land and forest areas into Life Zones;
- summary of organic matter or organic carbon storage information for tropical ecosystems using original source materials;

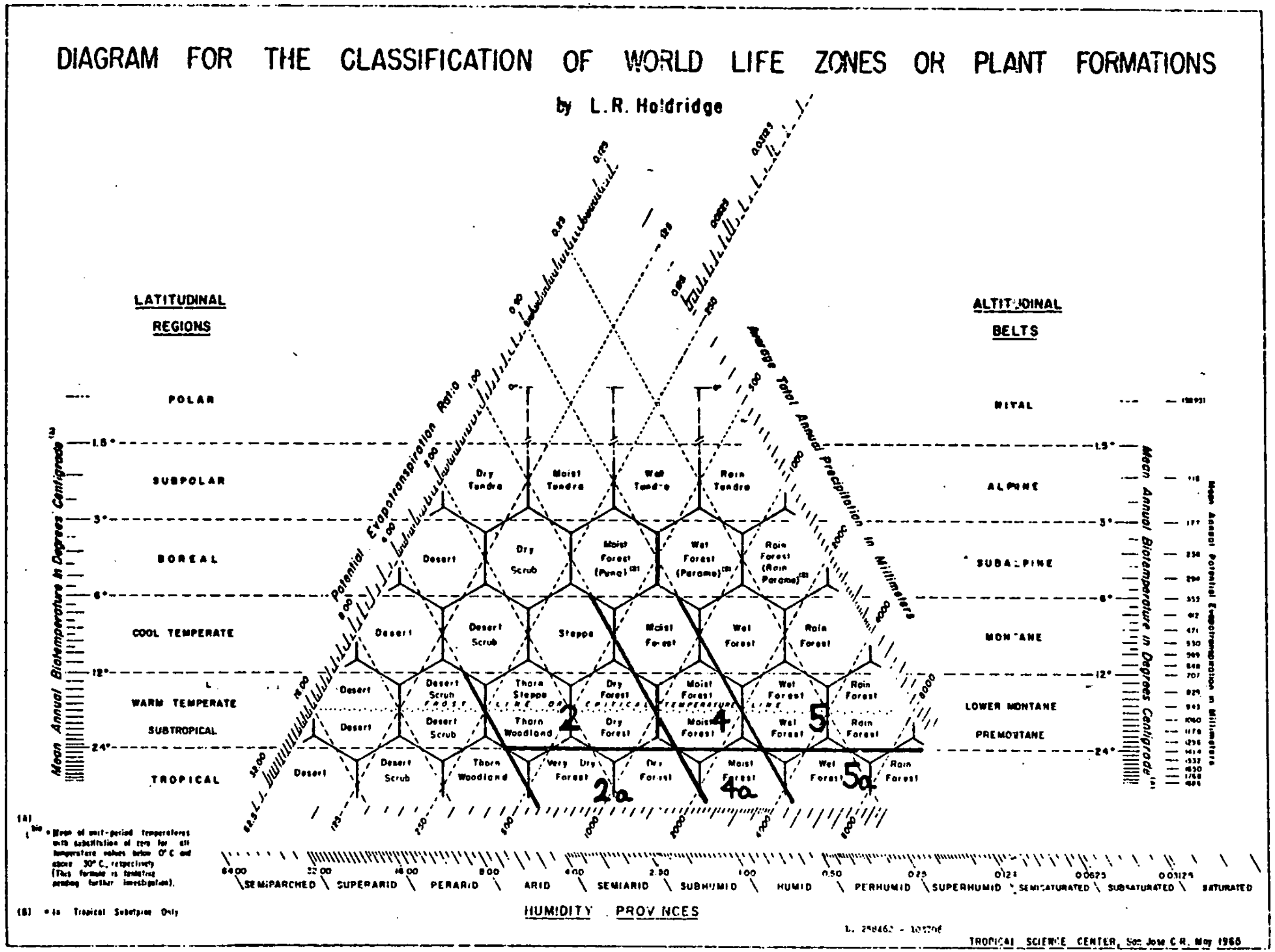

Fig. 1. Diagram for the classification of World Life Zones. The numbers 2a, 4a, 5a, 4, and 5 represent a grouping of Life Zones as discussed in the text.

- designation of Life Zone to each ecosytem for which data are available;
- multiplication of average organic carbon storage estimates for each Life Zone by the area of that Life Zone in the tropics; and
- addition of the Life Zone's organic carbon storage estimates in order to arrive at a weighted estimate of organic carbon storage in tropical forest ecosystems.

The estimates given in this paper are preliminary because we have not exhausted all the sources of information and because our estimates of Life Zone areas are yet to be completed. Details of calculations are given in the text and table footnotes.

Results

Definition of the Tropics

The delineation of tropical lands by the geographic limits set by the tropics of Cancer and Capricorn is convenient and expedient. However, ecosystems with tropical attributes may be found beyond these geographic limits due to the environmental conditions that prevail where they grow. Environmental gradients of solar energy input, light periodicity, temperature, moisture, and wind contribute to the latitudinal gradients of vegetation that typify our planet. Tropical ecosystems exist at one extreme of these latitudinal environmental gradients. Of all the environmental factors that are involved, frost is perhaps the one that separates the largest number of species. Lowland tropical species are not frost resistant and the distribution of many lowland tropical taxa show sharp limits along the transition between locations where frost occurs and frost-free environments. For this reason we use the occurence of frost in the lowlands as a secondary indicator of the tropical environment (Fig. 2). Use of this definition enables much of India to be included in the tropics.

From the map in Fig. 2 we arrived at a total of 89 countries geographically distributed as follows: Africa 42 countries, Central America 17 countries, South America 10 countries, Asia 12 countries, and Oceania 8 countries.

Estimates of Land and Forest Areas in Tropical Countries

Four world summaries of land and forest areas were available to us. The earliest one was by Zon and Sparhawk (1923), followed by Persson (1974), Sommer (1976), and Unesco (1978). The three recent world summaries generally divide forests into closed forests (forest canopy covers more than 20% of the ground surface) and open forests (forest canopy covers 5-20% of the ground surface). Persson (1974) adds scrub and brushland as a residual category since the areas concerned often have forest characteristics. Summaries of information are given by country in Table 1 and by continent in Table 2. A cursory analysis of the information shows that:

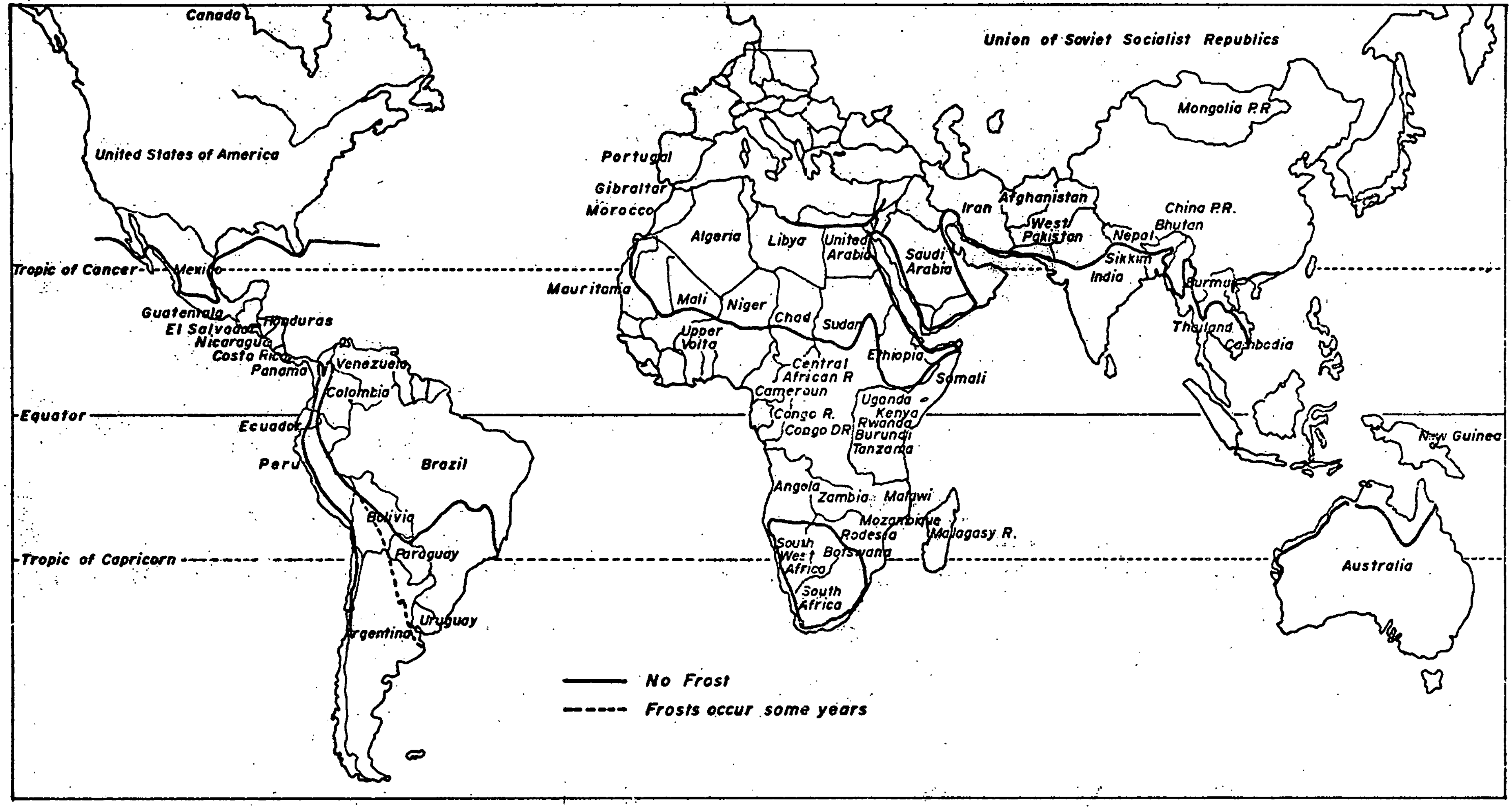

Fig. 2. Map of world showing the location of the frost-line. The definition of the tropics that we used is the area between the Tropics of Cancer and Capricorn plus any area between the Tropics of Cancer and Capricorn and the frost-line.

Table 1. Summary of forest areas for individual tropical countries as given by three different forest inventories.

	Area of Country			Total Area of All Forests			Percent of Land Area Covered By Forest		
	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (%)	Unesco
AFRICA									
Angola	1,260	1,247	1,250	41	727	430	3	58	34
Benin	107	113	110	11	68	50	11	60	45
Botswana	-	600	400	-	110	20	-	18	5
Burundi	-	28	30	-	3	-	-	11	-
Cameroon	495	475	480	142	300	300	29	63	63
C.A.E.	-	623	620	-	280	400	-	45	65
Chad	-	1,284	1,280	-	165	50	-	13	4
Congo	776	342	340	324	270	200	42	79	59
Equat. Guin.	25	28	30	18	20	20	74	71	67
Ethiopia	909	1,222	1,220	60	330	740	7	27	61
Gabon	-	268	270	-	245	200	-	92	74
Gambia	11	11	10	1	1	-	5	6	-
Ghana	207	239	240	99	120	190	48	50	79
Guinea	260	246	250	13	171	200	5	70	80

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered By Forest		
	Zon and Sparhawk	Persson	Unesco	Zon and Sparhawk	Persson	Unesco	Zon and Sparhawk	Persson	Unesco
		(10^3km^2)			(10^3km^2)			(%)	
Guinea Bissau	36	36	40	4	11	-	10	30	-
Ivory Coast	324	322	320	121	190	170	38	59	53
Kenya	629	583	580	13	19	90	2	3	16
Liberia	104	111	110	65	25	80	63	22	73
Madagascar	591	587	590	95	125	360	16	21	61
Malawi	113	118	120	1	70	20	1	59	17
Mali	-	1,240	-	-	45	150	-	4	12
Mauretania	-	1,031	1,170	0	150	-	-	15	-
Mauritius	-	2	20	-	0.3	20	-	17	100
Mozambique	1,103	783	780	76	665	40	7	85	5
Namibia	-	494	-	-	100	-	-	20	-
Niger	-	1,267	1,270	-	160	-	-	13	-
Nigeria	870	924	920	566	344	310	65	37	34
Reunion	3	3	-	0	1	-	1	40	-
Rhodesia	395	389	390	237	238	220	60	61	56
Rwanda	-	26	30	-	5	-	-	19	-

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered by Forest		
	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (%)	Unesco
Sao Tome	-	1	-	-	-	-	-	-	-
Senegal	190	196	200	4	45	120	2	28	60
Sierra Leone	88	72	70	1	4	70	1	5	100
Somalia	184	638	640	2	182	360	1	29	56
Sudan	3,541	2,506	2,510	28	420	130	1	17	5
Tanzania	1,024	940	950	39	390	700	4	42	74
Togo	88	56	60	1	36	50	2	64	83
Uganda	240	236	240	4	19	30	2	8	13
Upper Volta	-	274	270	-	10	50	-	4	19
Zaire	2,358	2,345	2,350	729	1,800	1,200	31	77	51
Zambia	754	753	750	452	373	370	60	50	49
TOTAL	16,688	22,659	22,150	3,145	8,245	7,340	19	37	33
ASIA									
Bangladesh	-	143	-	-	23	-	-	16	-

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered by Forest		
	Zon and Sparhawk	Persson ($10^3 km^2$)	Unesco	Zon and Sparhawk	Persson ($10^3 km^2$)	Unesco	Zon and Sparhawk	Persson (%)	Unesco
Brunei	-	6	10	-	6	10	-	96	100
Burma)		678	470	181	450	270	)	66	57
India)	2,830	2,153	1,720	872	648	470	) 35	30	27
Indonesia	2,142	1,904	1,900	940	859	1,220	44	45	64
Kampuchea Dem.	168	181	180	40	132	130	24	73	72
Laos	272	237	240	95	148	150	35	63	63
Malaysia	136	131	340	91	81	240	67	62	71
Sabah	80	76	-	77	60	-	96	79	60
Sarawak	109	125	-	87	95	-	80	76	-
Philippines	311	300	300	155	127	180	50	42	-
Sri Lanka	66	66	70	53	24	40	80	37	57
Thailand	630	514	510	142	290	310	23	56	61
Viet Nam	311	333	330	116	75	140	37	23	42
TOTAL	7,055	6,846	6,070	2,848	3,018	3,160	40	44	52

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered by Forest		
	Zon and Sparhawk	Persson	Unesco	Zon and Sparhawk	Persson	Unesco	Zon and Sparhawk	Persson	Unesco
		(10^3 km^2)			(10^3 km^2)			(%)	
CENTRAL AMERICA									
Bahamas	12	11	-	2	3	-	13	28	-
Belize	21	23	20	16	20	20	75	87	100
Costa Rica	48	51	50	36	22	40	75	43	90
Cuba	114	115	110	53	16	20	46	14	18
Domin. Rep.	50	49	50	39	11	20	77	23	40
El Salvador	21	21	20	4	13	-	18	61	-
Guadeloupe	3	2	-	0.3	1	-	12	38	-
Guatemala	125	109	110	81	65	70	65	60	64
Haiti	29	28	30	17	2	-	60	7	0
Honduras	120	112	110	96	70	70	80	63	64
Jamaica	11	11	10	3	5	-	30	45	-
Martinique	-	1	-	-	0.3	-	-	25	-
Mexico	993	986	850	225	350	160	23	35	19
Nicaragua	128	130	150	91	64	70	71	49	47
Panama	84	76	80	50	41	50	60	54	63

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered by Forest		
	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and	Persson (%)	Unesco
Puerto Rico	9	9	10	2	2	-	20	17	-
Trinidad	5	5	10	3	2	-	59	46	-
TOTAL	1,773	1,745	1,610	717	689	520	41	39	32
OCEANIA									
Australia	2,079	2,539	2,500	263	454	150	13	18	6
Fiji	19	18	-	5	13	-	25	68	-
New Caldeonia	18	19	-	2	3	-	11	14	-
New Hebrides	14	15	-	2	0.2	-	11	1	-
Papua-New Guinea	468	462	480	59	404	330	77	88	69
Samoa	3	3	-	2	2	-	70	64	-
Solomon Is.	44	28	-	22	26	-	50	86	-
Hawaiian Is.	17	-	-	4	-	-	25	-	-
TOTAL	2,661	3,086	2,980	658	901	480	25	29	16

Table 1. (continued).

	Area of Country			Total Area of All Forests			Percent of Land Area Covered by Forest		
	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (10^{3}km^2)	Unesco	Zon and Sparhawk	Persson (%)	Unesco
SOUTH AMERICA									
Boliva	1,332	1,099	1,100	518	500	450	39	46	41
Brazil	8,520	8,512	7,900	4,047	3,200	4,660	48	38	59
Colombia	1,228	1,140	1,140	607	780	650	54	68	57
Ecuador	307	284	280	233	181	220	76	64	79
Fr. Guiana	87	91	90	85	86	70	98	95	78
Guyana	232	215	210	202	182	190	87	85	90
Paraguay	313	407	200	150	210	150	58	52	75
Peru	1,770	1,285	1,290	907	650	700	51	51	54
Suriname	119	163	160	107	148	120	90	91	75
Venezuela	1,019	912	910	420	480	480	41	53	53
TOTAL	14,823	14,106	13,280	7,275	6,418	7,690	49	45	58

Table 2. Summary of the tropical forest areas given in the different estimates.

	Units	Africa	Central America	South America	Asia	Oceania	Total
Land area in tropics:							
Zon and Sparhawk 1923	$10^3 km^2$	15,688	1,773	14,823	7,055	2,661	43,000
Persson 1974	$10^3 km^2$	22,659	1,746	14,106	6,846	3,086	48,443
Sommer 1976	$10^3 km^2$	10,000	1,660	14,010	7,960	3,740	37,370
Unesco 1978	$10^3 km^2$	22,150	1,610	13,280	6,070	2,980	46,090
Total area of forests:							
Zon and Sparhawk 1923	$10^3 km^2$	3,145	717	7,275	2,848	658	14,624
Persson 1974	$10^3 km^2$	8,245	689	6,418	3,018	901	19,271
Sommer 1976	$10^3 km^2$	3,340	1,000	8,640	3,390	780	17,150
Unesco 1978	$10^3 km^2$	7,340	520	7,690	3,160	480	19,190
Area closed forests^a:							
Zon and Sparhawk 1923	$10^3 km^2$	-	-	-	-	-	-
Persson 1974	$10^3 km^2$	1,914	560	4,903	2,528	501	10,406
Sommer 1976	$10^3 km^2$	1,750	340	4,720	2,180	360	9,350
Unesco 1978	$10^3 km^2$	2,100	5,900	-	3,000	-	11,000
Area open woodlands and scrub^b:							
Zon and Sparhawk 1923	$10^3 km^2$	-	-	-	-	-	-
Persson 1974	$10^3 km^2$	6,331*	129	1,515*	490	400*	8,865*
Sommer 1976	$10^3 km^2$	-	-	-	-	-	-
Unesco 1978	$10^3 km^2$	5,240*	2,310*	-	600*	-	8,150*
Total forest to total land:							
Zon and Sparhawk 1923	%	19	41	49	40	25	34
Persson 1974	%	36	39	45	44	29	40

Table 2. (continued).

	Units	Africa	Central America	South America	Asia	Oceania	Total
Sommer 1976	%	33	60	62	43	21	46
Unesco 1978	%	33	32	58	52	16	42
<u>Closed forest to total land:</u>							
Zon and Sparhawk 1923	%	-	-	-	-	-	-
Persson 1974	%	8	32	35	37	16	22
Sommer 1976	%	18	21	34	27	10	25
Unesco 1978	%	6	55	-	34	-	--
<u>Open forest and scrub to total:</u>							
Zon and Sparhawk 1923	%	-	-	-	-	-	-
Persson 1974	%	28	8	10	7	13	18
Sommer 1976	%	-	-	-	-	-	-
Unesco 1978	%	27	-	3	18	-	-

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* By difference between total and closed forest areas.

[a] "Closed forest": land with trees whose crowns cover more than 20% of the area (Persson 1974).

[b] "Open forest" and "scrub" : land with trees whose crowns cover 5-20% of the area and residual category, respectively (Persson 1974).

- the area of the tropics given by the four world summaries are similar to each other with the exception of Sommer's estimate which is about 20% lower than the other three;

- the three recent world summaries report similar areas of tropical forests, but the early summary of Sparhawk and Zon gives a 20% lower estimate of tropical forests than the other three. Does this mean that the area of tropical forests has increased since the early part of this century or does it mean that the recent inventories are more complete?

- Africa contributes the largest land area to the tropics followed by Central and South America and Asia and Oceania (Persson 1974, Unesco, 1978);

- Africa and Central and South America have the largest forested areas which are about equal in size (Persson 1974, Unesco, 1978), however, Sommer's (1976) estimate shows that Africa contributes the least amount of forested area;

- the highest estimate of closed forested areas was reported by Unesco (1978), and the lowest estimate by Sommer (1976). Persson's (1974) estimate is approximately mid-way between these two extremes;

- tropical forests cover approximately 40% of the tropical land area;

- over half of the forested area in the tropics is covered by closed forests;

- although in general the forest inventories give similar results based on the total tropics, the forested areas of some individual countries vary significantly, e. g., Unesco estimates 61% of Ethiopia as being forested whereas Persson estimates 27%, and Unesco estimates 100% of Sierra Leone as being forested, whereas Persson estimates 5%. The major discrepancies between the forest inventories lie mainly within the African continent.

For the calculation of organic carbon storage in tropical forests we used the land and forest areas given by Persson (1974) because judging from the methodology for gathering information, he used the most reliable and thorough approach. These estimates correspond to approximate tropical forest areas around 1970.

According to Persson (1974, Table 2) the tropics comprise an area of 48,443 km^2 and of this, 19,271 km^2 or 40% are forested. Of this 19,271 km^2, 10,406 km^2 are closed forests, 7,394 km^2 are open forests, and 1,471 km^2 are scrub and brushlands (Persson 1974). This estimate is 28% and 20% lower than the respective estimates of Olson et al. (1978) and Whittaker and Likens (1973) and 16% higher than the estimate of Ajtay et al. (1979).

Classification of Land and Forest Areas into Life Zones

This aspect is the least reliable at this point. We began by estimating

Table 3. Percentage of each country located in each of the six groupings of Life Zones (c.f. Fig. 1).

	Tropical			Subtropical		
	Wet Forests(5a) (%)	Moist Forests(4a) (%)	Dry Forests(2a) (%)	Wet Forests(5) (%)	Moist Forests(4) (%)	Dry Forests(2) (%)
AFRICA						
Angola	-	25	-	-	5	70
Benin	-	-	-	-	-	100
Botswana	-	-	-	-	-	100
Burundi	2	30	68	-	-	-
Cameroon	5	30	65	-	-	-
C.A.E.	-	25	-	-	-	75
Chad	-	-	-	-	-	100
Congo	10	90	-	-	-	-
Equat. Guin.	-	100	-	-	-	-
Ethiopia	20	50	-	-	-	30
Gabon	15	70	15	-	-	-
Gambia	-	-	-	-	-	100
Ghana	-	30	70	-	-	-
Guinea	30	65	5	-	-	-
Guinea Bissau	-	-	-	-	-	100
Ivory Coast	-	40	60	-	-	-
Kenya	3	15	82	-	-	-
Liberia	30	60	10	-	-	-
Madagascar	-	-	-	-	50	50
Malawi	1	-	29	1	40	29
Mali	-	-	-	-	2	98

Table 3. (continued).

	Tropical			Subtropical		
	Wet Forests(5a) (%)	Moist Forests(4a) (%)	Dry Forests(2a) (%)	Wet Forests(5) (%)	Moist Forests(4) (%)	Dry Forests(2) (%)
Mauretania	-	-	-	-	-	100
Mauritius	-	-	-	-	100	-
Mozambique	-	-	-	2	30	68
Namibia	-	-	-	-	-	100
Niger	-	-	-	-	-	100
Nigeria	3	7	70	-	-	20
Reunion	-	-	-	-	100	-
Rhodesia	-	-	-	-	5	95
Rwanda	10	25	65	-	-	-
Sao Tome	-	100	-	-	-	-
Senegal	-	-	-	-	-	100
Sierra Leone	20	80	-	-	-	-
Somalia	-	-	-	-	-	100
Sudan	-	2	49	-	-	49
Tanzania	-	5	95	-	-	-
Togo	-	33	67	-	-	-
Uganda	-	10	90	-	-	-
Upper Volta	-	-	-	-	-	100
Zaire	20	65	15	-	-	-
Zambia	-	50	-	-	-	50

Table 3. (continued).

	Tropical			Subtropical		
	Wet Forests(5a) (%)	Moist Forests(4a) (%)	Dry Forests(2a) (%)	Wet Forests(5) (%)	Moist Forests(4) (%)	Dry Forests(2) (%)
ASIA						
Bangladesh	-	-	-	-	100	-
Brunei	-	100	-	-	-	-
Burma	-	-	-	24	51	25
India	-	-	-	10	50	40
Indonesia	30	65	5	-	-	-
Kampuchea Dem.	10	25	15	10	25	15
Laos	-	-	-	30	70	-
Malaysia) Sabah) Sarawak)	50	50	-	-	-	-
Philippines	18	18	-	24	40	-
Sri Lanka	-	25	75	-	-	-
Thailand	5	15	-	10	15	55
Viet Nam	10	15	5	20	35	15
CENTRAL AMERICA						
Bahamas	-	-	-	-	50	50
Belize	15	-	-	35	50	-
Costa Rica	66	27	7	-	-	-
Cuba	-	-	-	20	80	-
Domin. Rep.	-	-	-	22	55	23
El Salvador	-	-	-	-	28	71

Table 3. (continued).

	Tropical			Subtropical		
	Wet Forests(5a) (%)	Moist Forests(4a) (%)	Dry Forests(2a) (%)	Wet Forests(5) (%)	Moist Forests(4) (%)	Dry Forests(2) (%)
Guadeloupe	-	-	-	-	-	-
Guatemala	-	-	-	35	30	35
Haiti	-	-	-	-	-	-
Honduras	-	-	-	25	35	40
Jamaica	-	-	-	-	-	-
Martinique	-	-	-	-	-	-
México	-	-	-	5	25	70
Nicaragua	15	15	-	-	60	10
Panama	52	48	-	-	-	-
Puerto Rico	-	-	-	26	60	14
Trinidad	10	80	10	-	-	-
OCEANIA						
Australia	-	-	-	-	2	98
Fiji	-	-	-	-	100	-
New Caledonia	-	-	-	-	100	-
New Hebrides	-	-	-	-	100	-
Papua-New Guinea	66	34	-	-	-	-
Samoa	-	-	-	-	100	-
Solomon Is.	-	-	-	-	100	-
Hawaiin Is.	-	-	-	-	100	-

Table 3. (continued).

	Tropical			Subtropical		
	Wet Forests(5a) (%)	Moist Forests(4a) (%)	Dry Forests(2a) (%)	Wet Forests(5) (%)	Moist Forests(4) (%)	Dry Forests(2) (%)
SOUTH AMERICA						
Bolivia[a]	3	5	-	10	41	3
Brazil	10	35	15	5	20	5
Colombia	30	42	28	-	-	-
Ecuador[a]	11	44	17	22	6	-
Fr. Guiana	50	50	-	-	-	-
Guyana	27	43	30	-	-	-
Paraguay	-	-	-	-	50	50
Peru[a]	37	19	5	6	5	-
Suriname	-	85	15	-	-	-
Venezuela[a]	23	34	43	-	-	-

[a] Do not include desert, desert scrub, puna, paramo and tropical tundra Life Zones which accounts for about 5% of tropical South America.

the percentage of each tropical country that is located in each of six groupings* of Life Zones (Table 3). We then multiplied the area of each country by the approximate percentage cover of each Life Zone grouping. For 18 of the 89 tropical countries we had maps showing their Life Zone composition (Table 4). For those countries for which Life Zone maps were not available, we approximated their Life Zone composition using climatic and world atlases, vegetation maps, and our own knowledge of many of the tropical countries.

In this approximation we made no effort to differentiate Life Zones along altitudinal gradients. When this is done the final organic carbon storage estimate may change due to differences in organic carbon storage between high altitude forests and lowland forests.

The area of each Life Zone grouping for each tropical country was added and summarized by continent (Table 5). This preliminary estimate of tropical land area, classified according to Life Zone groupings, shows that 52% is Tropical or Subtropical Dry Forest, 35% is Tropical or Subtropical Moist Forest, and only 13% is Tropical or Subtropical Wet and Rain Forest. Subtropical Dry Forest covers the largest area (37%) of the tropics and Subtropical Wet and Rain Forests the smallest area (3%).

In order to assign a Life Zone designation to forested areas, we used Persson's data in Table 2 which shows the percent forested area by continent and Table 5 which shows the percent Life Zone distribution by continent. We arrived at Table 6 by performing the calculations indicated therein.

Summary of Organic Carbon Storage in Tropical Life Zones

The amount of organic carbon in tropical ecosystems was estimated from original sources of information. Sources dealing with vegetation generally expressed results in organic matter units. We converted organic matter units into organic carbon units using a conversion factor of 0.5. Sources dealing with soil generally expressed the results in units of organic carbon. Summarizing information of this type is accompanied by the usual problems of age variations among sites, lack of consistency in the reporting of data, papers with incomplete information, inconsistency in methodology, and so on. Reports from very young stands were omitted from the summary.

Experimental sites were classified according to Life Zone using information given by authors. When the information was incomplete we located the sites on maps and obtained climatic information from climatic atlases or other climatic information sources.

All the available sources of organic matter or organic carbon storage in above and below ground vegetation are summarized in Table 7, in soil in Table 8,

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* The six groupings of Life Zones (shown in Fig. 1) are:

Tropical Rain and Wet Forests, Tropical Moist Forests,
Tropical Dry Forests, Subtropical Rain and Wet Forests,
Subtropical Moist Forests, and Subtropical Dry Forests.

Table 4. Detailed Life Zone maps available for tropical countries.

Country	Scale	Source
Bolivia	-	Unzueta 1975
Colombia	1:1,000,000	Espinal and Montenegro 1963
Costa Rica	1:750,000	Tosi 1969
Dominican Republic	1:250,000	Tasaico 1967
Ecuador	1:1,000,000	Instituto Ecuatoriano de Reforma Agraria y Colonización
El Salvador	1:1,000,000	Holdridge 1977
Guatemala	1:1,000,000	Holdridge et al. 1978
Haiti	1:500,000	OAS 1972
Honduras	1:1,000,000	Holdridge 1962a
Mozambique	-	Soares and Barreto 1972
Nicaragua	1:1,000,000	Holdridge 1962b
Nigeria	1:3,000,000	Tosi 1968a
Panama	1:500,000	Tosi 1971
Paraguay	1:3,000,000	FAO 1969
Peru	1:1,000,000	Tosi 1968b
Puerto Rico	-	Ewel and Whitmore 1973
Thailand	1:500,000	Holdridge et al. 1971
Venezuela	1:2,000,000	Ewel et al. 1968

Table 5. Distribution of Life Zones in the tropics.

	Units	Tropical			Subtropical		
		Wet Forest (5a)[a]	Moist Forest (4a)[a]	Dry Forest (2a)[a]	Wet Forest (5)[a]	Moist Forest (4)[a]	Dry Forest (2)[a]
Africa	$10^3 km^2$	980	4,440	4,649	17	688	11,885
	%	4	20	21	-	3	52
Asia	$10^3 km^2$	868	1,652	188	658	2,091	1,390
	%	13	24	3	10	31	20
Central America[b]	$10^3 km^2$	97	74	4	159	544	819
	%	6	4	<1	9	32	48
South America[c]	$10^3 km^2$	2,028	4,441	2,178	650	2,163	458
	%	17	37	18	5	18	4
Oceania	$10^3 km^2$	305	157	-	-	134	2,488
	%	10	5	-	-	4	81
TOTAL	$10^3 km^2$	4,278	10,764	7,019	1,484	5,620	17,040
	%	9	23	15	3	12	37

[a] Refer to Fig.1 for explanation of this notation.

[b] Does not include Haiti, Jamaica, Guadeloupe or Martinique.

[c] 11% of tropical South America falls in the Warm Temperate Life Zones broken down as follows: 392 x $10^3 km^2$ as Dry Forest, 369 x $10^3 km^2$ as Moist Forest, and 6 x $10^3 km^2$ as Wet Forest. 4% of total land is classified as tropical and subtropical desert, desert scrub, puna, paramo and tundra.

Table 6. Designation of tropical forest into Life Zones.

	Units	Africa	Central America	South America	Asia	Oceania	Total
Open forests[a]:	$10^3 km^2$	5,666	18	930	407	373	7,394
Ratio ST-Dry/T-Dry	%/%	2.48	All ST	0.22	6.67	All ST	
Area ST-Dry	$10^3 km^2$	4,036	18	168	354	373	4,949
Area T-Dry	$10^3 km^2$	1,630	-	762	53	-	2,445
Closed forests[b]:	$10^3 km^2$	1,914	560	4,903	2,528	501	10,406
Ratio ST-Wet and Moist/T-Wet and Moist	%/%	0.13	4.10	0.43	1.11	0.27	
Area ST-Wet and Moist	$10^3 km^2$	213	450	1,474	1,329	107	3,573
Area T-Wet and Moist	$10^3 km^2$	1,701	110	3,429	1,199	394	6,833
Ratio ST-Moist/ST-Wet	%/%	All moist	3.56	3.6	3.10	All moist	
Area ST-Moist	$10^3 km^2$	213	351	1,154	1,005	107	2,830
Area ST-Wet	$10^3 km^2$	-	99	320	324	-	743
Ratio T-Moist/T-Wet	%/%	5.00	0.67	2.18	1.85	0.5	
Area T-Moist	$10^3 km^2$	1,418	44	2,351	778	131	4,722
Area T-Wet	$10^3 km^2$	283	66	1,078	421	263	2,111

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[a] The open forests (Persson 1974) were assumed to be equivalent to dry forest life zones.

[b] The closed forests (Persson 1974) were assumed to be equivalent to moist and wet forest life zones.

Table 7. Organic matter storage in the plant compartment.

Life Zone[a]	Age (yr)	Organic Matter (mt/ha)			Source
		Above Ground	Below[b] Ground	Total	
T-Lower Montane Rain Forest:	Mature	505	63	568	Edwards and Grubb 1977
	Mature	310	40	350	Edwards and Grubb 1977
T-Wet Forest:	Mature	322	60	382	Hozumi et al. 1969
T-Premontane Wet Forest:	Virgin	326	50[c]	376	Folster et al. 1976
	Virgin	179	28[c]	207	Folster et al. 1976
	16	203	31[c]	234	Folster et al. 1976
	27	197[d]	30[c]	227	Kellman 1970
	Mature	271	13	284	Golley et al. 1975
T-Moist Forest:	Mature	334	32	366	Ogawa et al. 1965
	Mature	513	25	538	Huttel and Bernhard-Reversat 1975, Huttel 1975
	Mature	380	42	422	Bhandu et al. 1973
	Virgin	243	48	291	Muller and Nielsen 1965
	Mature	340	56	396	Brunig et al. 1979, Jordan and Uhl 1978, Stark and Spratt 1977
	Mature	309	132	441	Klinge cited in Jordan and Uhl 1978
	Mature*	377	104	481	Klinge and Herrera 1978
	Mature*	192	97	289	Klinge and Herrera 1978
	Mature*	147	120	267	Klinge and Herrera 1978
	Mature*	85	138	223	Klinge and Herrera 1978
	Mature	316	11	327	Golley et al. 1975
T-Premontane Moist Forest:	50	305	54	359	Greenland and Kowal 1960
	Mature	431	24	455	Huttel and Bernhard-Reversat 1975, Huttel 1975
	?	406	67	473	Klinge cited in Edwards and Grubb 1977, Fittkau and Klinge 1973

Table 7. (continued).

Life Zone[a]	Age (yr)	Organic Matter Above Ground (mt/ha)	Organic Matter Below[b] Ground (mt/ha)	Organic Matter Total (mt/ha)	Source
	Mature	320	41[e]	361	Freson et al. 1974
	?	146	35	180	Bandhu et al. 1973
	Mature	330	43[e]	373	Nye and Greenland 1960
	?	286	37[e]	323	Enright 1979
ST-Lower Montane Rain Forest:	Mature	76	32[f]	108	Dugger 1978
ST-Wet Forest:	Mature	237	116	353	Crow 1980
	Mature	228	97[f]	325	Jordan 1971
	Mature	198	73	271[g]	Odum 1970, Ovington and Olson 1970
ST-Moist Forest:	?	144	16	160	Ogawa et al. 1965
	Mature	268	25	293	Ogawa et al. 1965
	?	169	17[h]	184	Dugger 1978
	60	205	34	239	Bhandu 1973
ST-Dry Forest:	Mature	39	6[i]	45	Lugo et al. 1978
	60	186	32	219	Ramam 1975
	?	69	10	79	Ogawa et al. 1965

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[a] T = Tropical

ST = Subtropical

Footnotes to Table 7 (continued).

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

[c] Estimated as follows: mean root/shoot for the T-Rain and Wet Forest=0.15 (S.E.=0.02). Organic matter storage in roots was calculated by multiplying the above ground organic matter storage by the root/shoot ratio.

[d] Mean of two sites and dry weight was assumed to be half fresh weight.

[e] Estimated as follows: mean root/shoot for the T-Moist Forest=0.13 (S.E.=0.02). Organic matter storage in roots was calculated as in footnote "c".

[f] Estimated as follows: mean root/shoot for the ST-Rain and Wet Forest=0.42. Organic matter storage in roots was calculated as in footnote "c".

[g] Mean of three plots and includes an estimate of small root (<5mm diam) biomass (Odum 1970).

[h] Estimated as follows: mean root/shoot for the ST-Moist Forest=0.10. Organic matter storage in roots was calculated as in footnote "c".

[i] Estimated as follows: mean root/shoot for the ST-Dry Forest=0.16 (S.E.=0.01). Organic matter storage in roots was calculated as in footnote "c".

* Caatinga (Amazon) association.

Table 8. Organic carbon content in soil compartment.

Life Zone [a]	Soil (mtC/ha)	Depth (cm)	Source
T-Premontane Rain Forest:	36.4	100	Holdridge et al. 1971
	57.6	100	Holdridge et al. 1971
	60.9	100	Holdridge et al. 1971
	50.3	100	Holdridge et al. 1971
	366.8	76	Jenny 1950
T-Lower Montane Rain Forest:	97.9	100	Holdridge et al. 1971
	120.7	100	Holdridge et al. 1971
	151.2	100	Holdridge et al. 1971
	599	100	Edwards and Grubb 1977
T-Montane Rain Forest:	96.9	100	Holdridge et al. 1971
T-Wet Forest:	58.3	100	Holdridge et al. 1971
	50.0	100	Holdridge et al. 1971
	13.8	100	Holdridge et al. 1971
	24.8	100	Holdridge et al. 1971
	35.0	100	Holdridge et al. 1971
	47.7	100	Holdridge et al. 1971
	38.0	100	Holdridge et al. 1971
	80.3	100	Holdridge et al. 1971
	37.1	100	Holdridge et al. 1971
	73.5	100	Holdridge et al. 1971

Table 8. (continued).

Life Zone [a]	Soil (mtC/ha)	Depth (cm)	Source
	34.5	100	Holdridge et al. 1971
	41.9	100	Holdridge et al. 1971
	72.2	100	Holdridge et al. 1971
	54.5	50	Folster et al. 1976
	93.5	50	Folster et al. 1976
	87.5	50	Folster et al. 1976
	78.5	50	Folster et al. 1976
	56.0	50	Folster et al. 1976
T-Premontane Wet Forest:	184.0	100	Holdridge et al. 1971
	60.7	100	Holdridge et al. 1971
	148.2	100	Holdridge et al. 1971
	144.0	100	Holdridge et al. 1971
	89.2	100	Holdridge et al. 1971
	41.0	100	Holdridge et al. 1971
	452.0	127	Jenny 1950
T-Lower Montane Wet Forest:	99.3	100	Holdridge et al. 1971
T-Moist Forest:	75.4	100	Yoda and Kira 1969
	85	50	Huttel and Bernhard-Reversat 1975
	50	50	Huttel and Bernhard-Reversat 1975

Table 8. (continued).

Life Zone [a]	Soil (mtC/ha)	Depth (cm)	Source
	51.4	103	Klinge 1975
	48	?	Bandhu et al. 1973
	48	10	Lundgren 1978
	100.1	100	Holdridge et al. 1971
	63.2	100	Holdridge et al. 1971
	58.1	100	Holdridge et al. 1971
	45.2	100	Holdridge et al. 1971
	104.3	100	Holdridge et al. 1971
	59.9	100	Holdridge et al. 1971
	48.1	100	Holdridge et al. 1971
T-Premontane Moist Forest:	43.8	30	Greenland and Kowal 1960
	35.0	50	Huttel and Bernhard-Reversat 1975
	125.0	100	Klinge et al. 1975
	154.6	100	Holdridge et al. 1971
	86.6	100	Holdridge et al. 1971
T-Lower Montane Moist Forest:	114.6	100	Holdridge et al. 1971
T-Dry Forest:	109.0	100	Holdridge et al. 1971
	101.3	100	Holdridge et al. 1971
	7.8	100	Holdridge et al. 1971
	28.2	100	Holdridge et al. 1971

Table 8. (continued).

Life Zone [a]	Soil (mtC/ha)	Depth (cm)	Source
	26.1	100	Holdridge et al. 1971
	56.9	100	Holdridge et al. 1971
	57.9	100	Holdridge et al. 1971
ST-Wet Forest:	73.2	30	Odum 1970
ST-Lower Montane Wet Forest:	30	30	Tanner 1977
	80	40	Tanner 1977
	250	45	Tanner 1977
	90	40	Tanner 1977
ST-Moist Forest:	37.4	100	Yoda and Kira 1969
	88.9	100	Yoda and Kira 1969
	64.8	50	Bandhu 1973
	89.6	50	Singh 1979
	45.9	50	Singh 1979
	59.2	50	Singh 1979
	44.8	50	Singh 1979
	18.2	30	Singh 1979
ST-Dry Forest:	24.2	100	Yoda and Kira 1969

[a] T=Tropical

ST=Subtropical

and in litter in Table 9. We report the data in these three tables in their original form (either organic matter or organic carbon).

To determine if there is a relationship between organic matter storage in vegetation and Life Zone we quantified a specific Life Zone using the potential evapotranspiration to precipitation ratio (PET/P) as follows: we assumed that the mean organic matter storage of a particular Life Zone occurred at the mid-point of the hexagon, i. e. at the mid-precipitation and temperature values. We then determined the PET/P ratio from the Life Zone chart. The location of the mid-point for each of the forested Life Zones and the corresponding PET/P ratio is shown in Fig. 3. Low PET/P ratios (0.16-0.39) correspond with wet Life Zones and high ratios (greater than 1) correspond with dry Life Zones. The mean plant biomass for those Life Zones with more than two data points (Table 7) is linearly correlated with the PET/P ratio (r^2=0.7) as shown in Fig. 4. This graph suggests that the wetter Life Zones store more organic matter in the vegetation than the drier Life Zones.

Mean soil organic carbon storage (Table 8) was also plotted against the PET/P ratio (Fig. 5) resulting in a curvilinear relationship (r^2=0.6). This suggests that organic carbon storage in the soil in very wet Life Zones is high and decreases rapidly towards the moist to dry Life Zones.

When summarized by the six groupings of Life Zones the organic carbon storage in tropical forests show the following trends (Table 10):

- total ecosystem organic carbon storage decreases from the tropics to the subtropics and with decreasing moisture (Fig. 6);
- above ground plant organic carbon storage does not decrease along the moisture gradient, although it does decrease from tropical to subtropical Life Zones;
- judging from the coefficients of variation (26-54%), wet and moist Life Zone groupings do appear to store discreet amounts of organic carbon;
- the organic carbon storage in plants of the ST-Dry Forest is the most variable (coefficient of variation = 81%);
- with the exception of the Subtropical Rain and Wet Forest, roots account for a small proportion (10-17%) of the total plant organic carbon storage;
- organic carbon storage in litter varies little among the Life Zone groupings and accounts for only 1-4% of the total organic carbon storage of the Life Zone groupings;
- total plant organic carbon storage ranges from 55-70% of the total organic carbon storage of the Life Zone groupings.

Table 9. Organic matter storage in the litter compartment.

Life Zone[a]	Organic Matter			Source
	Leaves	Wood	Total	
		(mt/ha)		
T-Premontane Rain Forest:			4.5	Jenny et al. 1949
T-Lower Montane Rain Forest:	7.7	10.9	18.6	Edwards and Grubb 1977
	5.5	0.9	6.5	Edwards and Grubb 1977
T-Premontane Wet Forest:			15.9	Jenny et al. 1949
			4.8	Golley et al. 1975
T-Moist Forest:			1.8	Yoda and Kira 1969
			5.6	Greenland and Kowal 1960
			6.0	Klinge 1976
			11.3	Klinge 1975
	6.6	3.9	10.4[b]	Klinge and Herrera 1978
	5.4	5.0	10.4[b]	Klinge and Herrera 1978
	7.2	15.1	22.3[b]	Klinge and Herrera 1978
	6.2	3.9	10.1[b]	Klinge and Herrera 1978
	2.7	6.5	9.2	Bhandhu et al. 1973
			5.5	Bartholomew et al. 1953
			8.0	Bartholomew et al. 1953
			7.3	Bartholomew et al. 1953
	3.4[c]	14.6[c]	18.0	Golley et al. 1975
T-Premontane Moist Forest:	7.2	18.2	25.4	Klinge et al. 1975
			3.3	Malaisse et al. 1975
			2.3	Greenland and Kowal 1960
			6.5	Malaisse et al. 1975
ST-Lower Montane Rain Forest:			3.5	Dugger 1978
ST-Wet Forest:			6.0	Odum 1970
ST-Moist Forest:			7.8	Dugger 1978
			7.7	Bandhu 1973

Table 9. (continued).

Life Zone [a]	Organic Matter			Source
	Leaves	Wood	Total	
	(mt/ha)			
			2.6	Yoda and Kira 1969
			3.0	Yoda and Kira 1969
ST-Dry Forest:	-	-	7.2	Lugo et al. 1978
	7.6	2.0	8.7	Lugo et al. 1978
	2.6	1.2	3.8	Lugo et al. 1978
	-	-	7.3	Ramam 1975
			3.4	Yoda and Kira 1969

[a] T= Tropical

ST= Subtropical

[b] = Caatinga (Amazon) association

[c] = Weighted mean of dry and wet season values according to length of seasons.

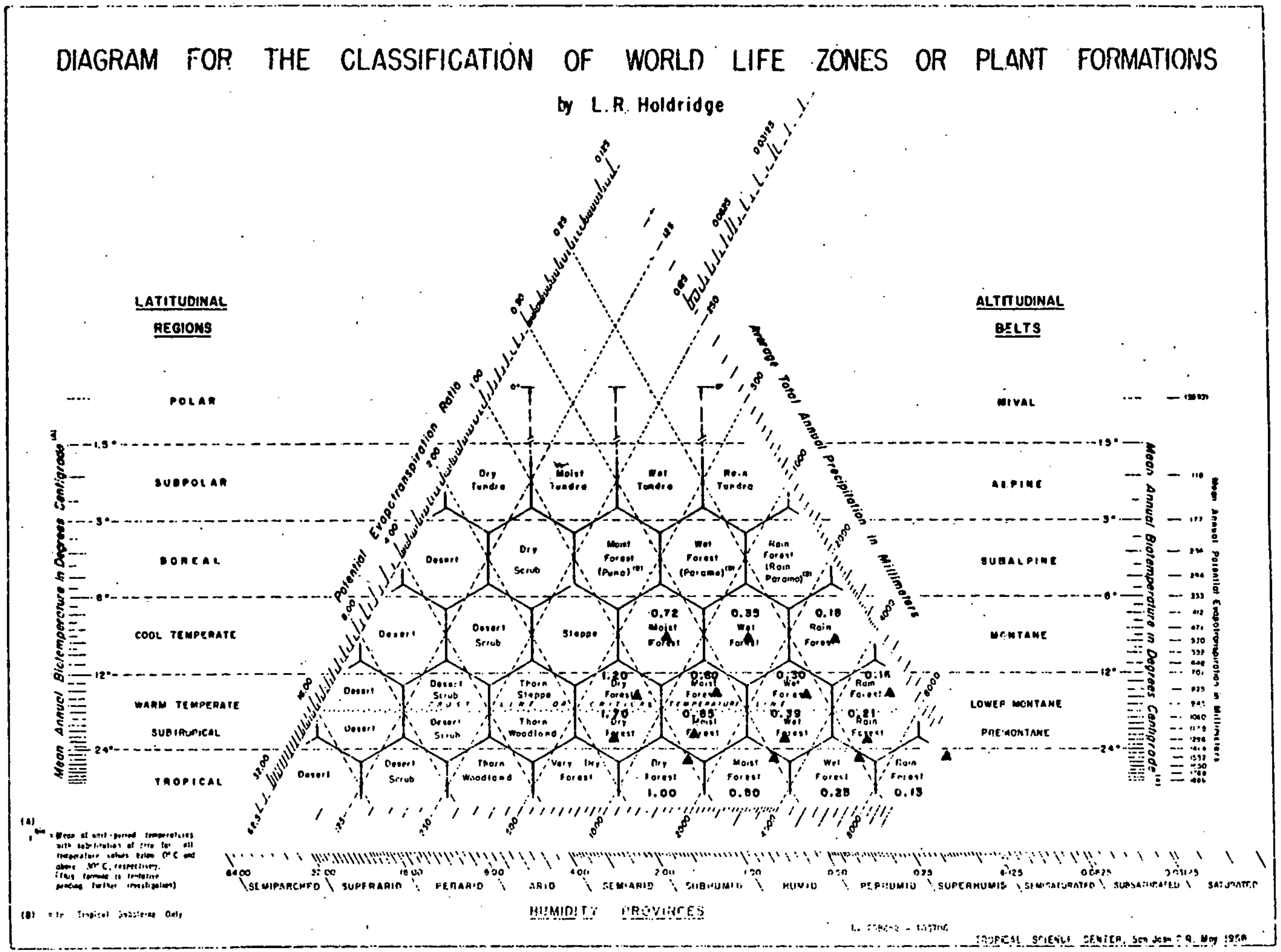

Fig. 3. Location and value of the potential evapotranspiration to precipitation ratio (PET/P) for the mid-Life Zone conditions. These ratios are used to quantify a Life Zone.

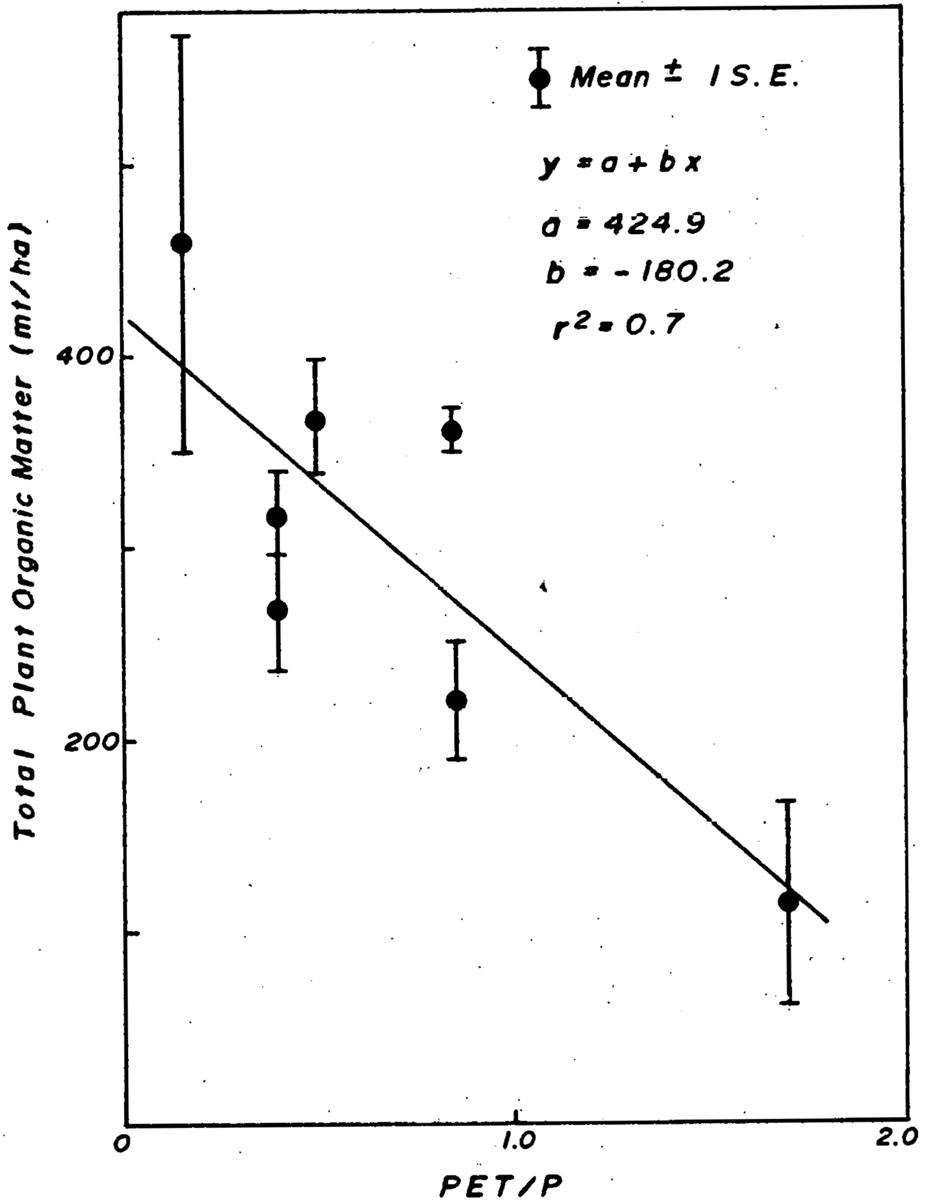

Fig. 4. Relationship between total plant organic matter storage by Life Zone and PET/P ratio. See Fig. 3. for location and value of the ratios for the mid-Life Zone conditions.

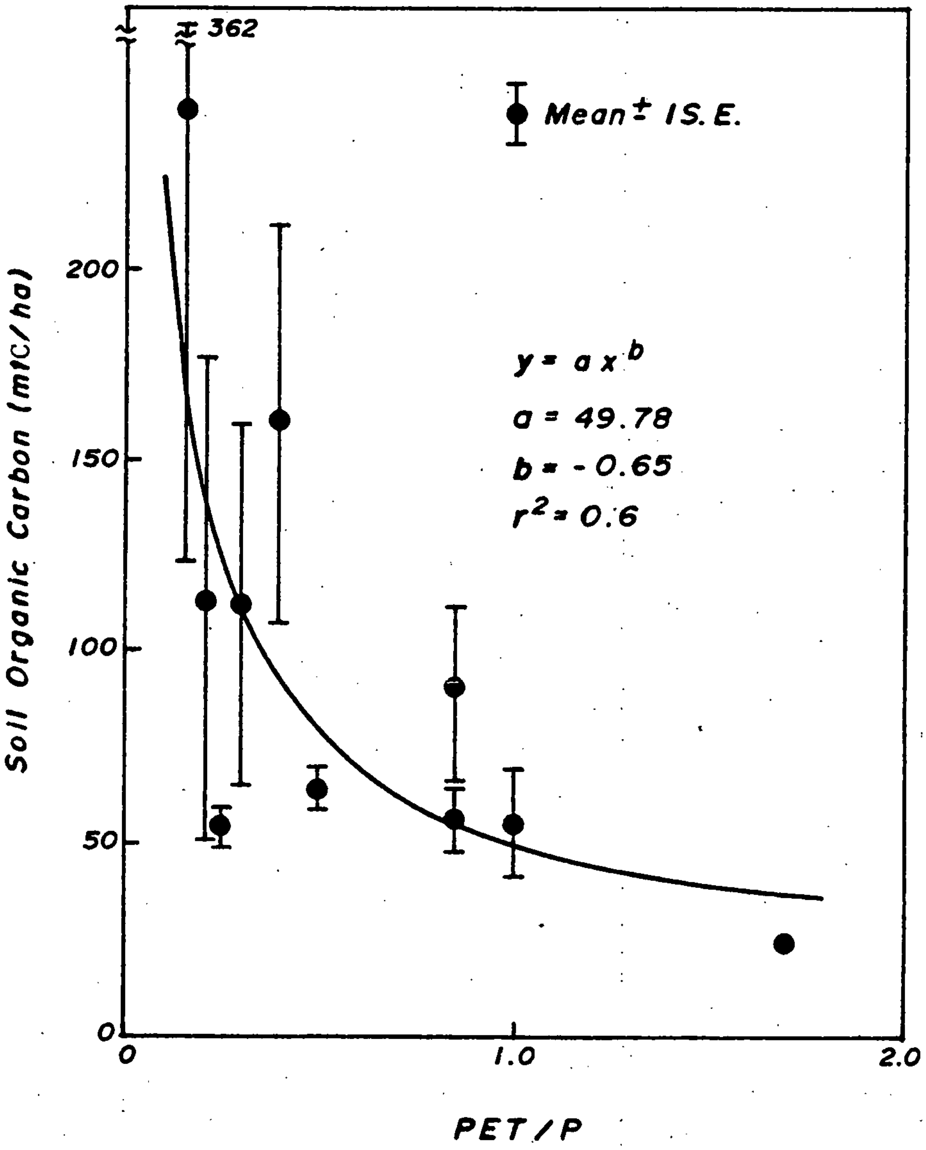

Fig. 5. Relationship between soil organic carbon storage by Life Zone and PET/P ratio. See Fig. 3. for the location and value of the ratios for the mid-Life Zone conditions.

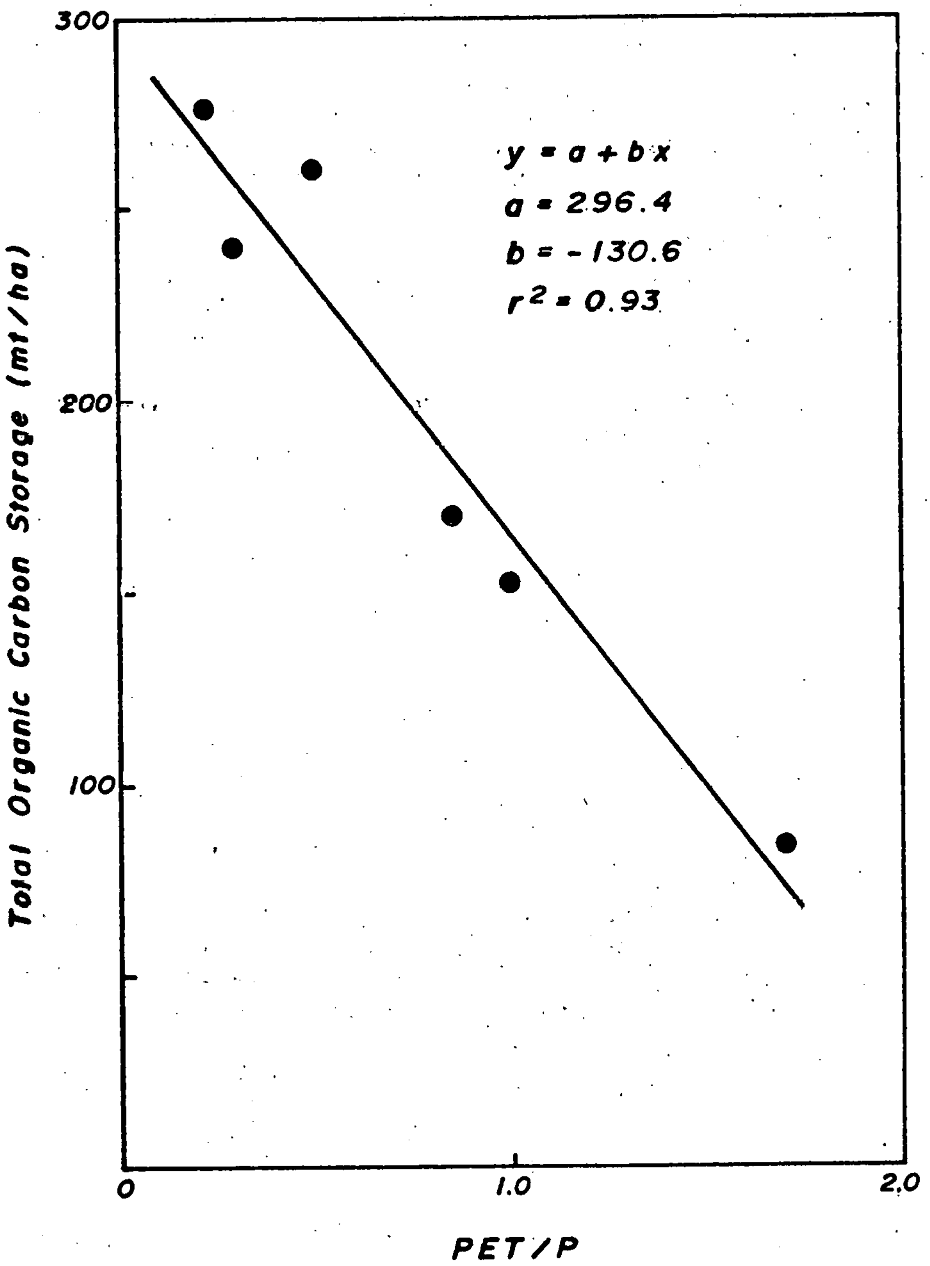

Fig. 6. Relationship between total organic carbon by Life Zone grouping and the PET/P ratio. See Fig. 3 for location and value of the ratios for the mid-Life Zone conditions.

Estimate of Total Organic Carbon Storage in the Tropical Forests

A weighted and preliminary estimate of the total amount of organic carbon stored in tropical forests was obtained by multiplying the land areas of forested Life Zones (Table 6) by the average total organic carbon storage in each Life Zone (Table 10). The total amount of organic carbon stored in tropical forest ecosystems is 325 billion metric tons or about 650 billion mt of organic matter (Table 11). Of this, 33% is stored in the Subtropical Life Zones. Although 42% of the forested area is in the Dry Forest Life Zones, only 24% of the organic carbon is stored there. Wet and Rain Forests account for 23% of the total storage of organic carbon while Moist Forests store the largest amount of organic carbon (53%). Unfortunately, the Moist Forests are the Life Zones that support the highest intensity of human activity and are those that succumb quicker to deforestation (Tosi and Voertman 1964).

Any estimate of the organic carbon stored in the tropics has a range of uncertainty based on the uncertainty in estimates of the area and of the organic carbon stored in the Life Zones. As yet, we do not have enough information to estimate the uncertainty in the area estimates. However, we can arrive at an estimate of the uncertainty based on the organic carbon storage in the Life Zones. The mean organic carbon storage in plants and in soil, plus and minus one standard error, is given in Tables 12 and 13, respectively. The range of values of organic carbon storage based on one standard error, represent 17% of the mean for plants and 22% of the mean for soil.

Discussion

Our final estimate of organic carbon storage in tropical forests contrasts sharply with other estimates (Tables 14 and 15). Ours is the lowest of all. The estimate of organic carbon storage in plants obtained by Whittaker and Likens (1973) is almost double our estimate, and those of Ajtay et al. (1979) and Olson et al. (1978) are only slightly larger than ours (Table 14). Olson et al.'s and Schlesinger's (1979) estimate for organic carbon stored in soils are more than double our estimate, whereas Ajtay et al.'s estimate is closer to ours. The differences between our estimate and that of others are due to:

- differences in definition of the tropics - ours is broader due to the inclusion of the frost-free boundary;

- differences in estimates of the area of tropical forests - Whittaker and Likens and Olson et al. use higher estimates and Ajtay et al. use 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 Likens' area estimate) is for the present. The difference between these two estimates has been suggested to have resulted from deforestation of the tropical forests. This difference of 970 million ha represents about 1.6% deforestation/yr for the whole tropics. However, recent estimates of deforestation put the value at 0.4-0.6%/yr

Table 10. Organic carbon storage in the tropical Life Zones. 1. S. E. is given in parenthesis.

Life Zone[a]	n	Above Ground	Below Ground	Total Plant	n	Soil	n	Litter	Total Forest
		(mtC/ha)[b]				(mtC/ha)		(mtC/ha)	
T-Rain and Wet Forest	8	145 (18.6)	20 (3.1)	164 (21.0)	36	106.5 (20.3)	5	5.0 (1.5)	276
T-Moist Forest	18	152 (12.7)	31 (4.6)	182 (11.1)	19	73.5 (7.6)	17	4.8 (0.8)	260
T-Dry Forest	-	-	-	91[c]	7	55.3 (14.5)	-	5.5[c]	152
ST-Rain and Wet Forest	4	92 (13.6)	40 (9.1)	132 (27.5)	5	104.6 (37.8)	2	2.4	239
ST-Moist Forest	4	98 (13.5)	11 (2.1)	110 (14.8)	8	56.1 (8.8)	4	2.6 (0.7)	169
ST-Dry Forest	3	49 (22.4)	8 (4.0)	57 (26.0)	-	24.2	5	3.0 (0.5)	84

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[a] T = Tropical
ST = Subtropical

[b] Assumed carbon content = 0.5 x organic matter.

[c] We found no plant biomass data for Tropical Dry Forest. We assumed the ratio of the organic carbon storages of the T-Dry Forest to the T-Moist Forest was the same as the ratio of organic carbon storages for the ST-Dry to ST-Moist Forests of 0.5. Organic carbon storage T-Dry Forest = 0.5 x 182 = 91. Carbon storage in litter was calculated by a similar method.

Table 11. Organic carbon storage in the tropics.

Life Zone[a]	Area of Forest (10^6ha)	Total Storage (mtC/ha)	Total Carbon (10^9mt)	(%)
T-Wet Forest	211.2	276	58.3	18
T-Moist Forest	472.2	260	122.8	38
T-Dry Forest	244.5	152	37.2	11
ST-Wet Forest	74.3	239	17.8	5
ST-Moist Forest	283.0	169	47.8	15
ST-Dry Forest	494.9	84	41.6	13
TOTAL	1,780		325.5	100

[a] T = Tropical

ST = Subtropical

Table 12. Organic carbon storage in plants.

Life Zone[a]	Area (10^{6}ha)	Organic Carbon in Plants (mtC/ha ± 1SE*)	Total Organic Carbon in Plants (10^{9}mtC) - 1SE*	Mean	+ 1SE*
T-Rain and Wet Forest	211.2	164 ± 21	30.2	34.6	39.1
T-Moist Forest	472.2	182 ± 11	80.8	85.9	91.1
T-Dry Forest	244.5	91 ± 27[b]	15.7	22.3	28.9
ST-Rain and Wet Forest	74.3	132 ± 28	7.7	9.8	11.9
ST-Moist Forest	283.0	110 ± 15	26.8	31.1	35.4
ST-Dry Forest	494.9	57 ± 27	14.8	28.2	41.6
TOTAL	1,780		176.0	211.9	248.0

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[*] Standard Error.

[a] T = Tropical, ST = Subtropical.

[b] Because no SE was available for this value we used that for ST-Dry Forest.

Table 13. Organic carbon storage in soil.

Life Zone[a]	Area (10^6ha)	Soil Organic Carbon (mtC/ha ±1SE*)	Total Organic Carbon in Soil (10^9mtC)		
			- 1SE*	Mean	+ 1SE*
T-Rain and Wet Forest	211.2	106.5 ± 20.3	18.2	22.5	27.8
T-Moist Forest	472.2	73.5 ± 7.6	31.1	34.7	38.3
T-Dry Forest	244.5	55.3 ± 14.5	9.9	13.5	17.1
ST-Rain and Wet Forest	74.3	104.6 ± 37.8	5.0	7.8	10.6
ST-Moist Forest	283.0	56.1 ± 8.8	13.4	15.9	18.4
ST-Dry Forest	494.9	24.2 ± 14.5[b]	4.8	12.0	19.2
TOTAL	1,780		81.4	106.4	131.4

* Standard Error.

[a] T = Tropical, ST = Subtropical.

[b] Because no SE was available for this value we used that for T-Dry Forest.

Table 14. Estimates of organic carbon storage in plants in tropical forest ecosystems.

Source	For Year:	No of Forest Categories	Area of Forests (10^6ha)	Range of Organic Carbon Storage in Forests (mtC/ha)	Total Organic Carbon Storage in Plants (10^9mtC)
This study	early 1970's	6	1,780	57-182	212
Ajtay et al. 1979	1970's	3	1,480	113-189	244
Olson et al. 1978	1970	6	2,220	70-180	254
Rodin et al. 1975	b	3	5,535	54-220	674[a]
Whittaker and Likens 1973	1950	2	2,450	160-200	460

[a] Assumed C = 50% x organic matter.

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

Table 15. Estimates of organic carbon storage in soil in tropical forest ecosystems.

Source	Area (10^6ha)	Storage of Soil Organic Carbon (10^9mtC)
This study	1,780	106
Ajtay et al. 1979	1,480	123
Olson et al. 1978	2,220	307
Schlesinger 1979	2,450	288

(Seiler and Crutzen 1980), with values as high as 1.3% in high population density areas such as parts of Venezuela and 3%/yr in industrializing countries such as Costa Rica (Tosi, this volume). 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 the tropical forests and/or that Whittaker and Likens overestimated the area.

- 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. The conversion factor is generally critical only for conversion of organic matter in plants to organic carbon because most studies on soil measure carbon and not organic matter. Using the carbon content values in Table 5.4 in the paper by Ajtay et al. we calculate an average carbon content in forest living components and forest ecosystems to be 0.51, closer to our value.
- conceptual differences - with the exception of Olson et al. (1978) the other estimates ignored the variability in tropical environments by dividing the tropical forests into 2-3 categories.

We believe that our estimate overestimates the storage of organic carbon in the tropics because:

- the forest area estimate could be high as it reflects a 1970 survey;
- organic carbon storage values may be biased towards mature forests; and
- organic carbon storage information for montane forests and for tropical dry forests, when it becomes available, could affect the estimate.

If, indeed, our estimates are correct or if the real value is significantly lower than the value reported by others, then there are serious implications to the current interpretation of theory and models based on the high organic carbon storage values. For example:

- predictions of the impacts on the atmospheric CO_2 concentration by tropical deforestation would have to be tempered because the 1%/year estimate of Woodwell et al. (1978) if itself true, would represent a significantly lower contribution of carbon to the atmosphere (actually about 50% less);

- estimates of organic carbon turnover would have to be upgraded;
- estimates of organic carbon storage for other ecosystems would become questionable; and
- all budget or model calculations using the high storage estimates would have to be revised.

Need for research

In another paper (Brown, this volume) a similar summary of rates of organic production in different tropical Life Zones is presented. The implications of organic production along with these lower storage estimates to the role of tropical forests in the CO_2 balance of the world are also discussed. However, these and other considerations are limited by the data base. Figure 7 was prepared to show the distribution of ecosystem oriented data by Life Zones in the tropics. The large gap of information in the dry and montane forests is alarming.

This Fig. 7 is presented as a summary for granting agencies of the research needs in tropical lands.

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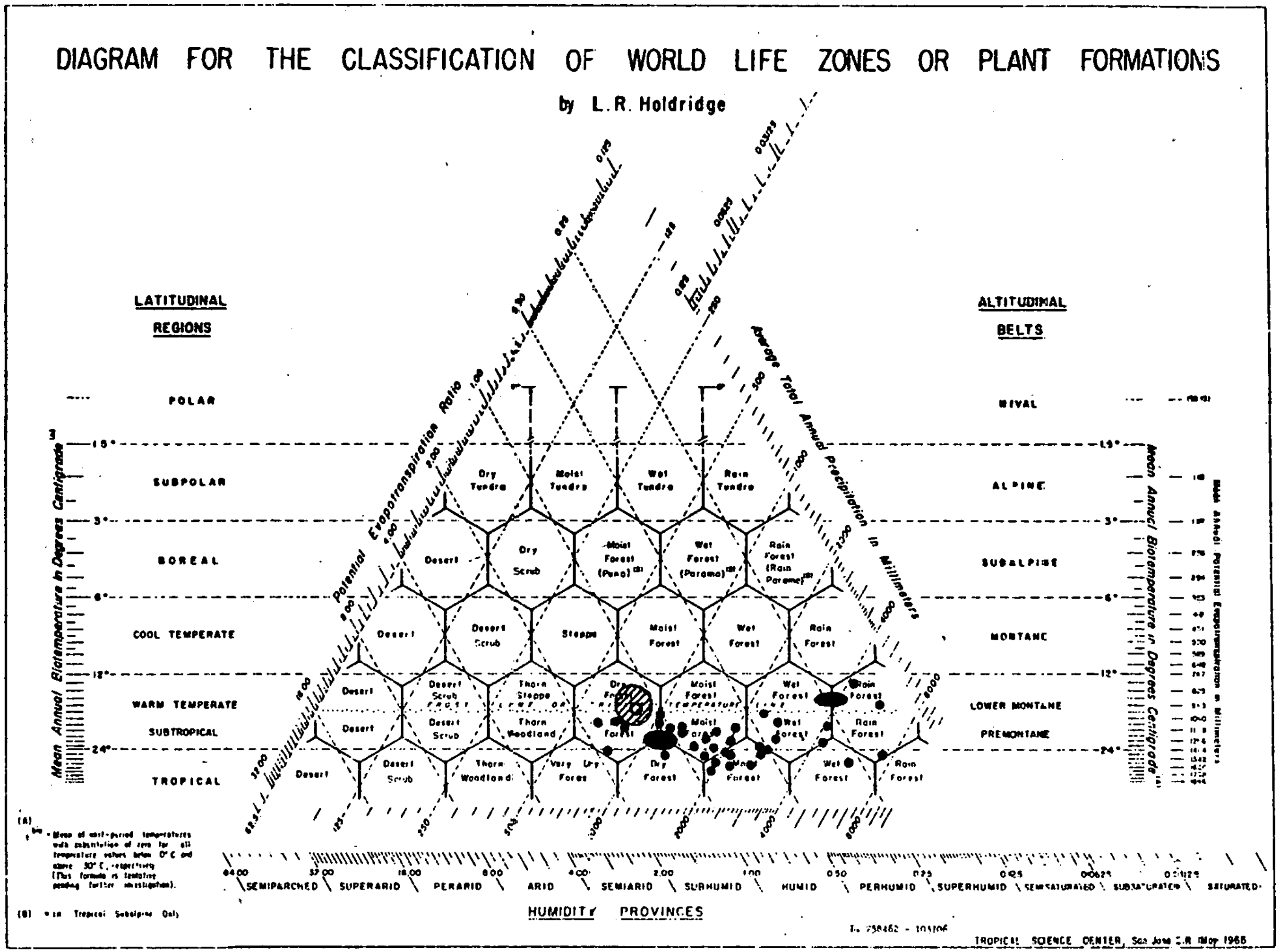

Fig. 7. Distribution of ecosystem oriented data from the tropics by Life Zone.

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RATES OF ORGANIC MATTER ACCUMULATION AND LITTER PRODUCTION IN TROPICAL FOREST ECOSYSTEMS

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Introduction

The role of tropical forest ecosystems in relation to the global carbon issue depends on three aspects: their area, the amount of organic matter stored in them, and the rate at which they accumulate organic matter. The area of tropical forests and the amount of organic matter stored in them are discussed in the paper by Brown and Lugo (this volume). This paper deals with the rate of organic matter accumulation in tropical forests and specifically addresses the question of organic matter production by Life Zone.

As a frame of reference, Fig. 1 shows the above ground biomass of different age stands of temperate forests (excluding plantations). Biomass (used synonomously with organic matter) accumulates fairly linearly from age 1 yr to about 50 yr, at which time above ground biomass is less than 150 mt/ha. Maximum above ground biomass for these 41 temperate forest stands is approximately 300 mt/ha at maturity. In contrast, Fig. 2 shows the above ground biomass for different age stands of tropical forests. Biomass in these tropical forests accumulates rapidly during the first 10-20 yr, at the end of which above ground biomass in many stands is approximately 100 mt/ha. In comparison, temperate forests had reached a biomass of only about 20 mt/ha at the end of 20 yr. By age 50 yr, some of the tropical stands had biomass values greater than 200 mt/ha. Many of the mature tropical forests had above ground biomass in excess of 300 mt/ha and several in excess of 400 mt/ha. The data presented in Figs. 1 and 2 support the notion that tropical forests reach higher biomass, faster and earlier than temperate forests.

Because of the high diversity of tropical Life Zones (Tosi, this volume) the rate of organic matter accumulation might be expected to vary with Life Zone. Some indication of this variation is seen in Fig. 2. Moist Forest Life Zones appear to reach a higher biomass earlier and have a higher biomass at maturity than the other Life Zones. In contrast, Dry Forest Life Zones have some of the lowest biomasses in both young and mature stands.

Organic Matter Accumulation by Life Zone

The trends in organic matter accumulation can be analyzed by Life Zone for

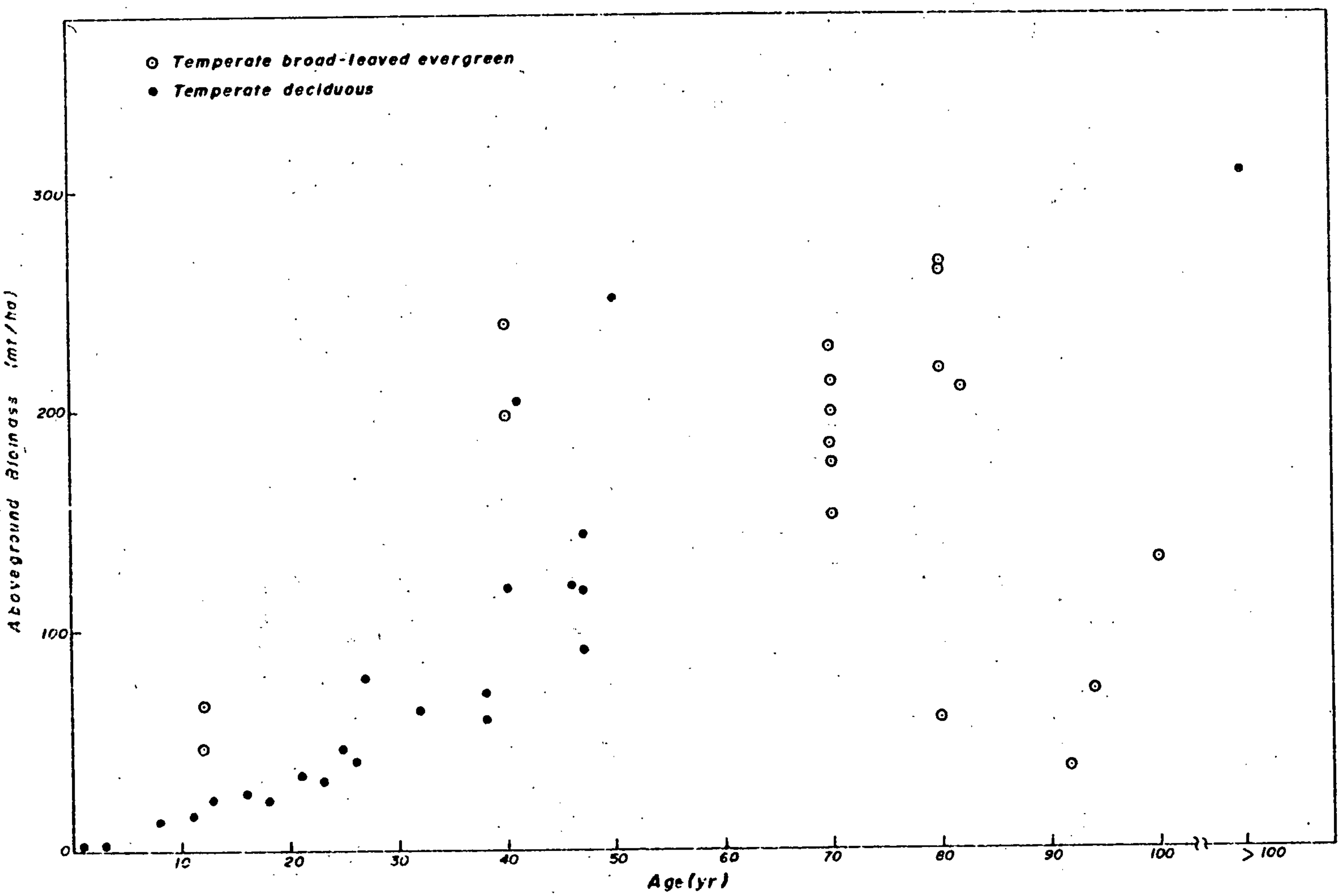

Fig. 1. Relationship between above ground biomass and stand age for temperate forests (data are from Art and Marks 1971).

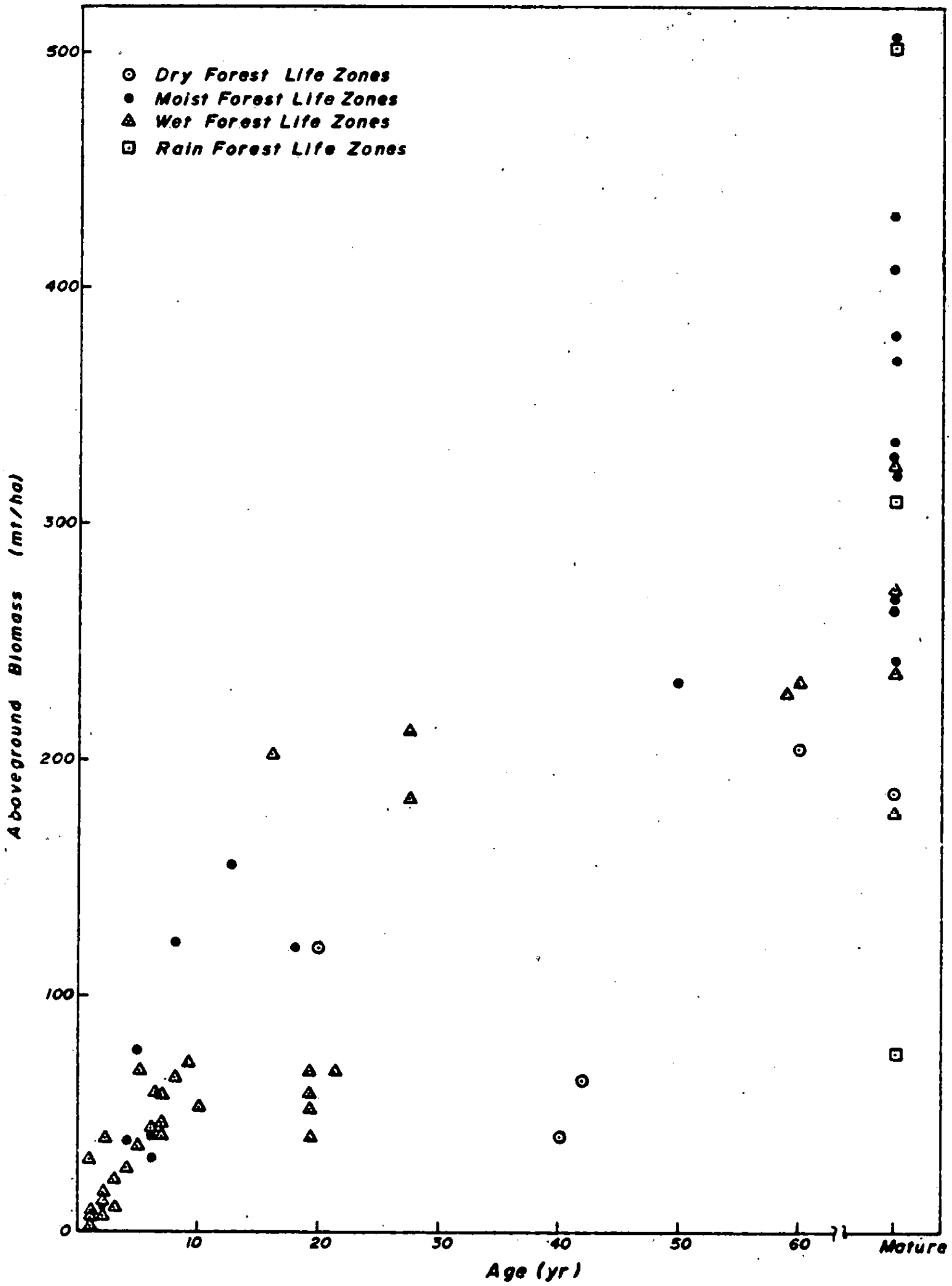

Fig. 2. Relationship between above ground biomass and stand age for tropical forests (data are from the sources in Table 7 of Brown and Lugo, this volume, and the following additional sources: Bartholomew et al. 1953, Christensen 1978, Ewel 1971, Lugo et al. 1974, Seth and Kaul 1978, Singh 1975, Snedaker 1970).

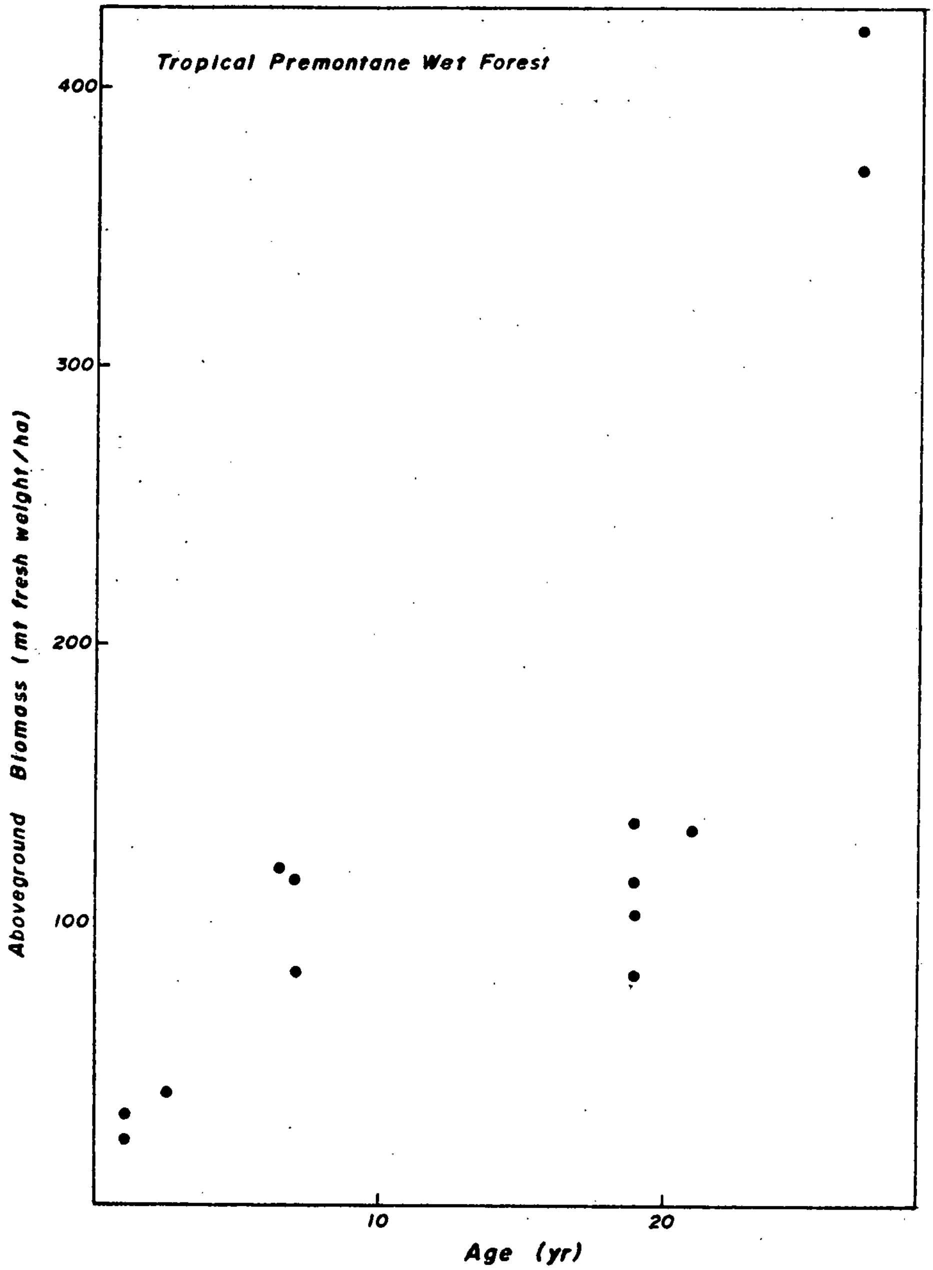

Fig. 3. Relationship between above ground biomass (fresh weight) and stand age in a Tropical Premontane Wet Forest Life Zone (data are from Kellman 1970).

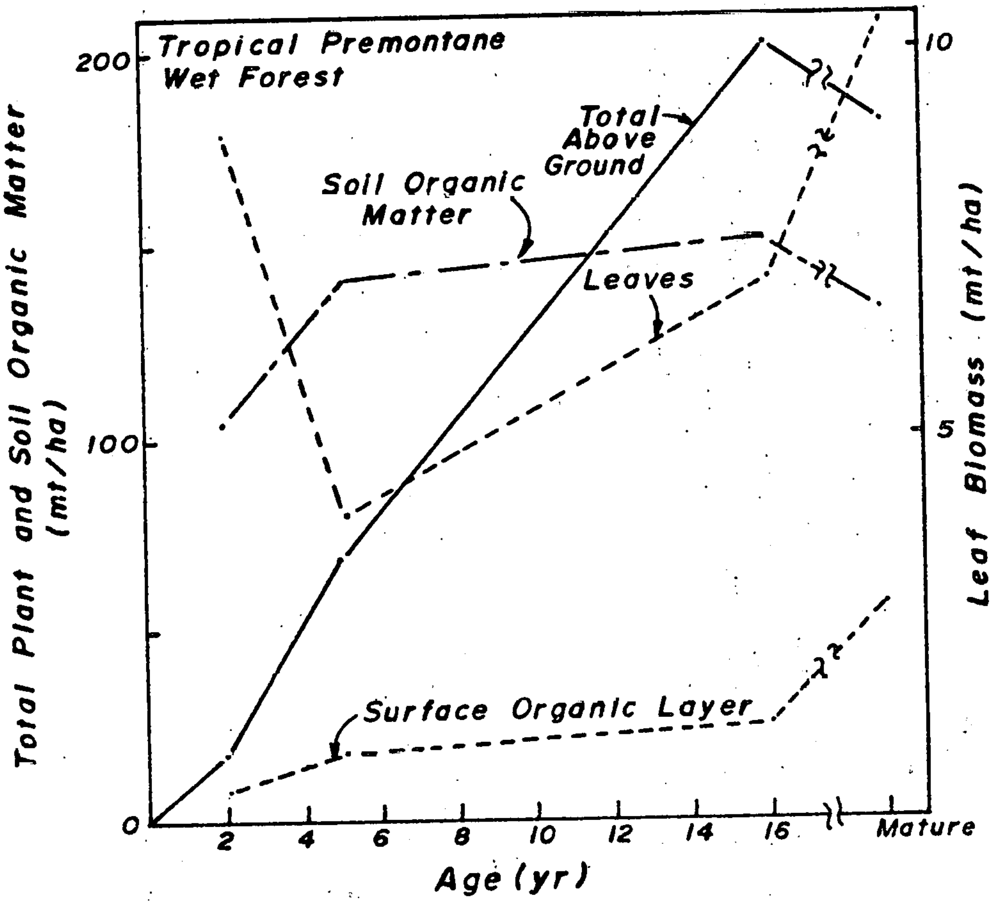

Fig. 4. Relationship between biomass of forest components and stand age in a Tropical Premontane Wet Forest Life Zone (data are from Folster et al. 1976).

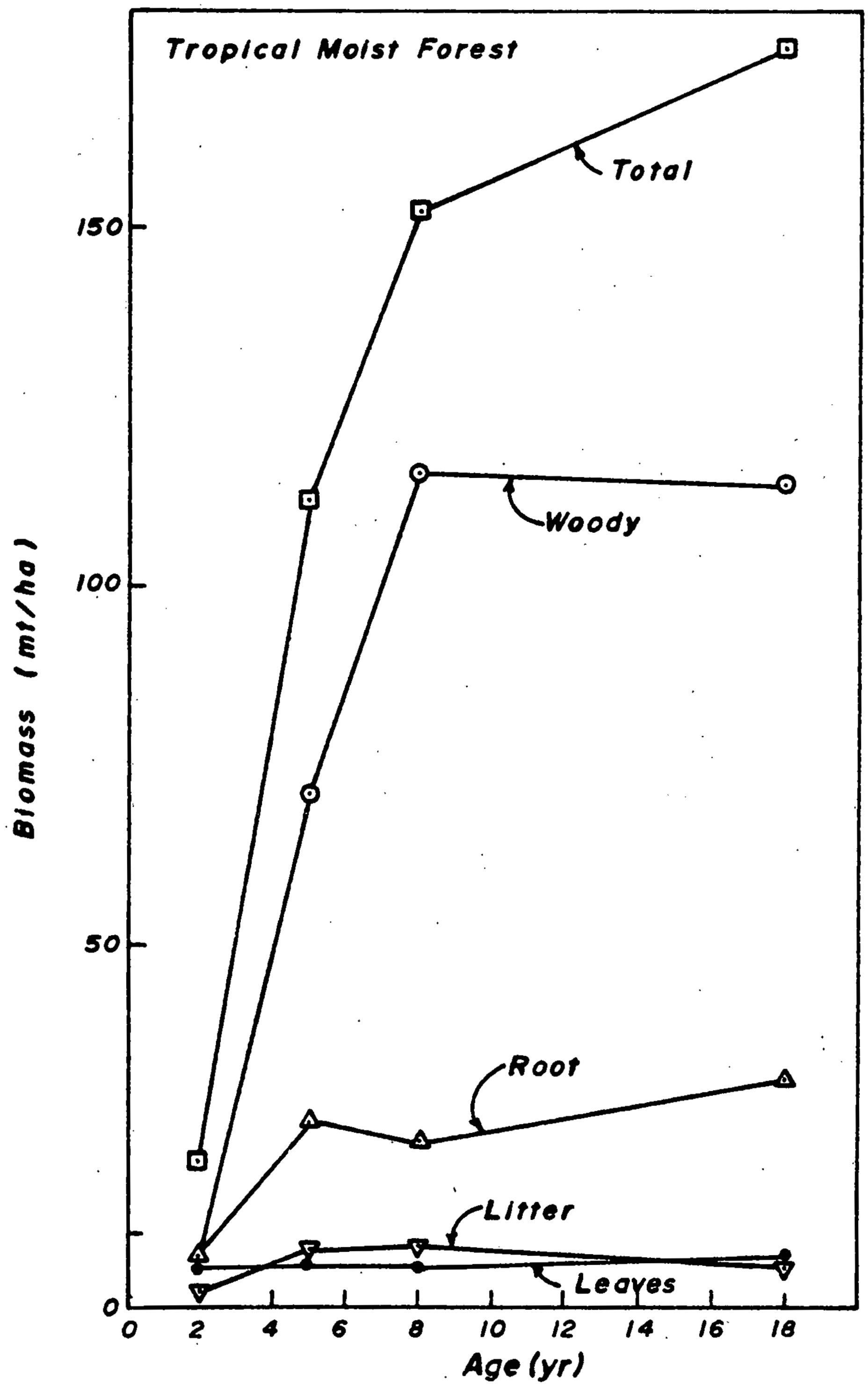

Fig. 5. Relationship between biomass of forest components and stand age in a Tropical Moist Forest Life Zone (data are from Bartholomew et al. 1953).

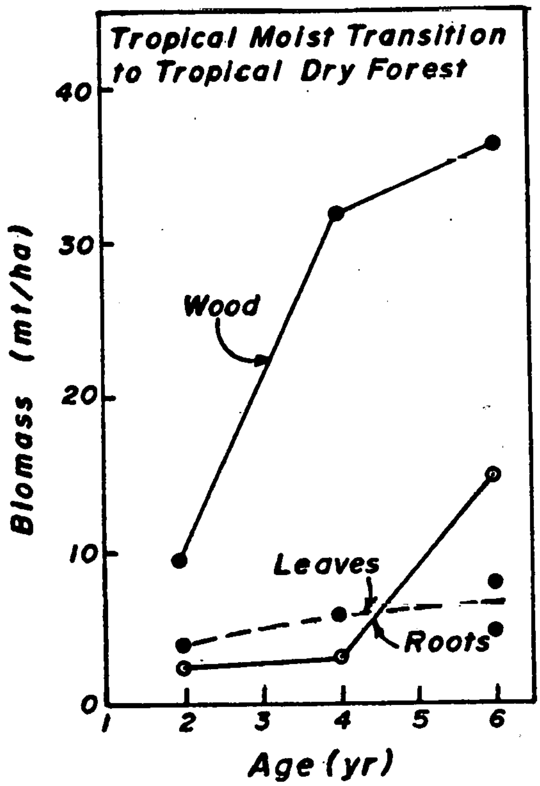

Fig. 6. Relationship between biomass of forest components and stand age in a Tropical Moist Transition to Tropical Dry Forest Life Zone (data are from Ewel 1971).

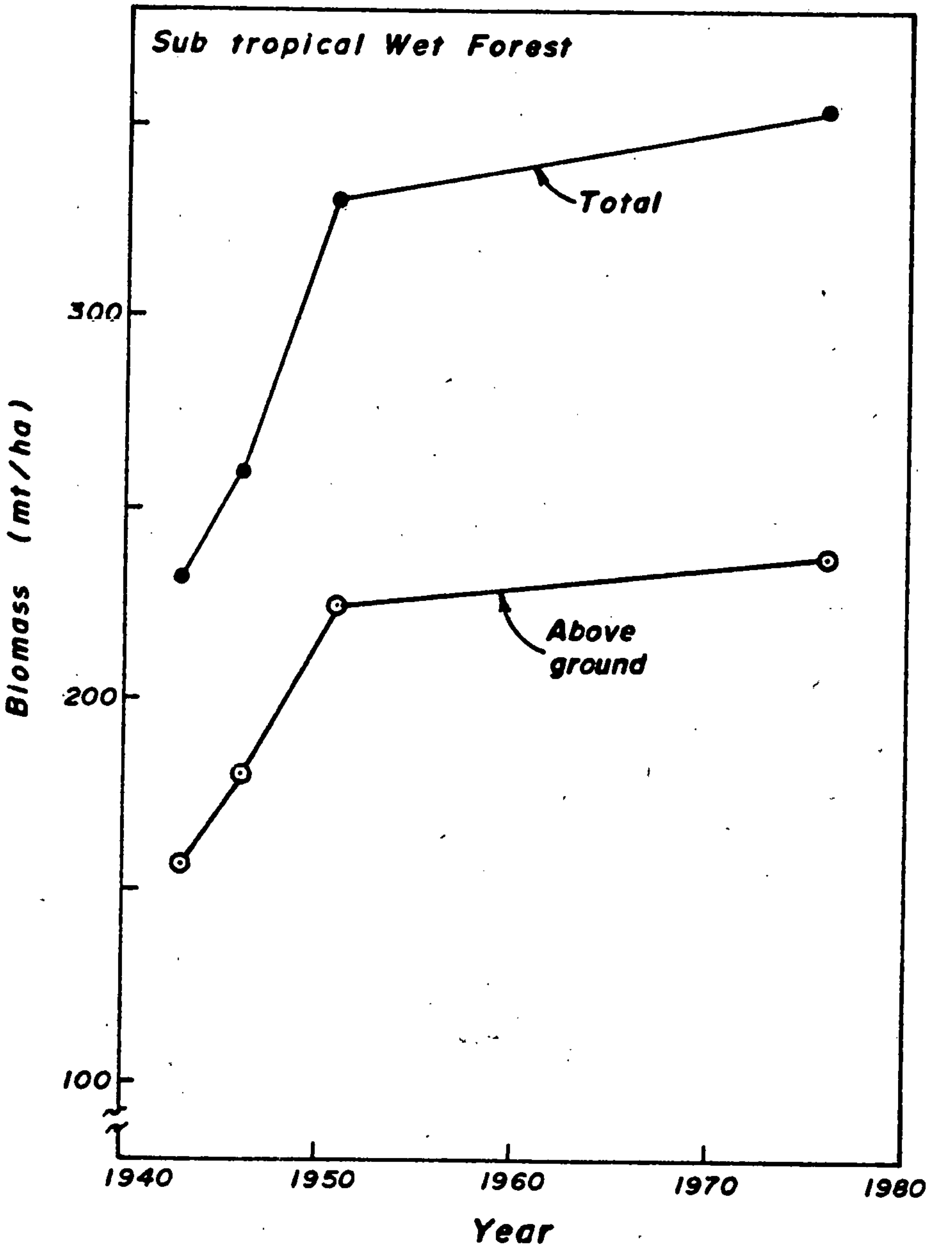

Fig. 7. Relationship between biomass of forest components and length of time after a natural disturbance in a Subtropical Wet Forest Life Zone (data are from Crow 1980).

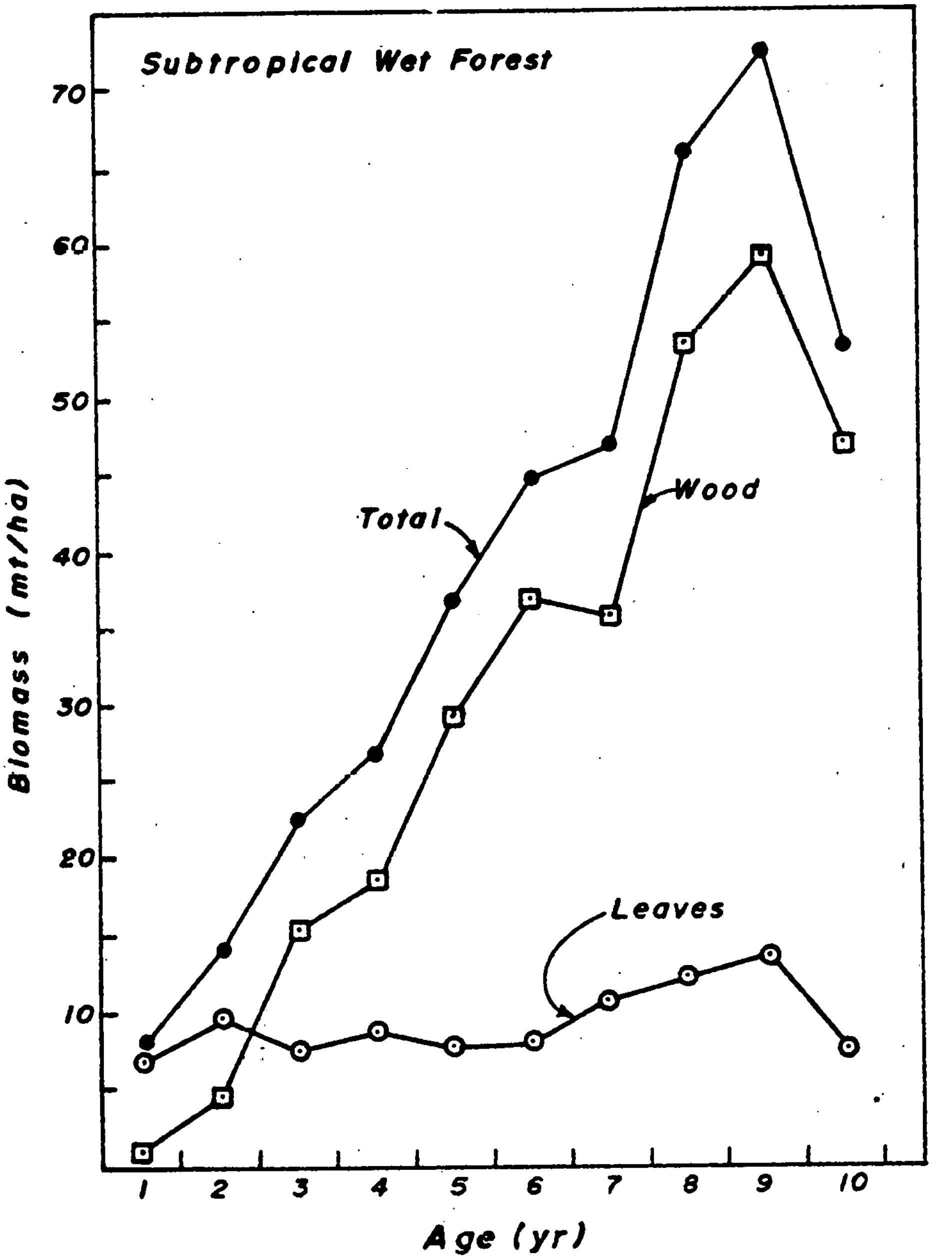

Fig. 8. Relationship between biomass of forest components and stand age in a Subtropical Wet Forest Life Zone (data are from Snedaker 1970).

those sites for which time series biomass data are available. Graphs of organic matter accumulation in Tropical Premontane Wet Forest, Tropical Moist Forest, and Subtropical Wet Forest Life Zones are shown in Figs. 3-8. On inspection, the following general trends can be observed:

- organic matter accumulates quickly and in some stands it takes about 20 yr for total biomass to be as high or almost as high as that of nearby mature forests (Figs. 4 and 5);
- leaf organic matter develops rapidly in the early years and changes little with age of the stand (Figs. 4, 5, 6, and 8);
- litter accumulates quickly in young stands and remains fairly constant as the stands mature (Figs. 4 and 5);
- soil organic matter appears to build up slowly with time (Fig. 4);
- during the first 6 yr above ground organic matter accumulates quickest in the Tropical Moist Forest (approximately 90 mt, Fig. 5), followed by the Tropical Premontane Wet Forest (approximately 75 mt, Fig. 4, and approximately 50 mt, Fig. 3), Tropical Moist Transition to Tropical Dry Forest (approximately 46 mt, Fig. 6), and Subtropical Wet Forest (approximately 44 mt, Fig. 8). I chose the first 6 yr for this comparison because all graphs had data up to this age. The Tropical Premontane Wet Forest in Fig. 4 is very close to the boundary of the Tropical Moist Forest hexagon. And, the rapidity with which this Forest and the Tropical Moist Forest (Fig. 5) accumulate organic matter may suggest that the climate conditions converging on the Tropical Moist Forest Life Zone are optimal for organic matter production.

No organic matter accumulation data were available for Tropical or Subtropical Dry Forest Life Zones. However, Ewel (1977) found that % 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.

Strategy of Organic Matter Accumulation

An analysis of the data of organic matter accumulation suggests that 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 (c.f. Fig. 6). This trend is also shown in Figs. 5 and 8. Although wood and roots are slower to develop, they are eventually the compartments that store a large proportion of the organic matter of a forest. Soil appears to accumulate organic matter at the slowest rate (c.f. Fig. 4). However, the soil compartment often stores almost as much organic matter as the sum of the above ground compartments (Brown and Lugo, this volume).

Litter Production in Tropical Life Zones

There is not enough information to do a thorough summary of net primary production. However, I am presently summarizing information on net above ground organic matter production. For example, I have 6 values of above ground wood production for Tropical Moist Forest, ranging from 3.0-7.5 mt/ha.yr (Greenland and Kowal 1960, Huttel and Bernhard-Reversat 1975, Jordan and Escalante 1980, Kira et al. 1967, Muller and Nielsen 1965), 1 value for Tropical Premontane Moist Forest of 4.6 mt/ha.yr (Huttel and Bernhard-Reversat 1975), and 1 value for a Subtropical Wet Forest of 2.4 mt/ha.yr (Odum 1970).

One component of above ground organic matter production for which data are abundant is litterfall. I found 51 litterfall data points, covering 11 Life Zones (Table 1). Only litter produced by the above ground plant parts is considered in this study. Total litterfall includes leaf, fruit and flowers, twigs, and branches; it does not include dead timber. As with the organic matter storage data, Tropical Rain and Dry Forest Life Zones are poorly represented.

To determine if a relationship exists between litterfall and Life Zone, I quantified the Life Zone location using the potential evapotransporation to precipitation ratio (PET/P) using the mid-precipitation and mid-temperature values of a given hexagon. For further details of this calculation and the resulting PET/P ratios see Brown and Lugo (this volume). The relationship between litterfall and PET/P is described by an inverse U-shaped curve (Fig. 9). Total litterfall is low for the very wet Life Zones (PET/P= 0.15-0.25), rises rapidly to the highest litterfall value in the Tropical Moist Forest Life Zone (PET/P= 0.50), and then declines gradually through the Premontane and Subtropical Moist Forests (PET/P= 0.85) to the lowest litterfall value in the Subtropical Dry Forest (PET/P = 1.7). Leaf and fruit litterfall generally follows the same trend as for total litterfall.

The high rate of litterfall in the Tropical Moist Forest is consistent with its high rate of organic matter accumulation (Fig. 5) and its high plant biomass (Brown and Lugo, this volume). This Life Zone covers a larger area than any other Life Zone in the tropics. Also, Tosi (this volume) showed that human populations concentrate in this climate. It appears that this Life Zone's high rate of production and rapid succession results in a larger carrying capacity for humans.

Rates of litterfall appear to reach steady state values very quickly in tropical forests (Figs. 10 and 11). In a Tropical Premontane Wet Forest (Fig. 10) litterfall reached a steady state value in less than 10 yr, and in a Subtropical Moist Forest between 10 and 15 yr (Fig. 11). The rapid establishment of this steady state is another indication of the rapid recovery of tropical forests following disturbance.

Litter Production in Tropical Forests

In steady state ecosystems the input of litter to the forest floor is balanced by losses, either through biotic processes such as microbial decomposition or by physical processes such as leaching. The amount of organic carbon that is available for export via the pathways suggested by Holdridge and by Lugo (this volume) is mainly related to the amount of litter produced.

Table 1. Litterfall for tropical forests.

	Litterfall		
Life Zone[a]	Leaf and Fruit	Total	Source
	(mt/ha.yr)		
T-Premontane Rain Forest:	-	8.52	Jenny et al. 1949
T-Lower Montane Rain Forest:	6.49	7.39	Edwards 1977
	6.60	7.93	Edwards 1977
	6.17	7.68	Edwards 1977
	6.15	7.22	Edwards 1977
T-Wet Forest:	8.94	12.02	Folster et al. 1976
	7.60	9.46	Folster et al. 1976
	6.76	8.74	Folster et al. 1976
T-Premontane Wet Forest:		10.48	Golley et al. 1975
		10.2	Jenny et al. 1949
		7.43	Kellman 1970
T-Moist Forest:	8.26	12.86	Bhandu et al. 1973
	9.83	11.37	Golley et al. 1975
	7.10	11.10	Haines and Foster 1977
	8.10	9.18	Huttel and Bernhard-Reversat 1975
	9.30	11.88	Huttel and Bernhard-Reversat 1975
	6.14	9.54	Jordan and Escalante 1980
	11.8	23.2	Kira et al. 1967
	6.50	-	Leigh and Smythe 1979
T-Premontane Moist Forest:	6.91	-	Cornforth 1970
	8.76	-	Enright 1979
	6.55	11.0	Fittkau and Klinge 1973
	4.63	-	Hopkins 1966
	7.17	-	Hopkins 1966
	8.18	9.62	Huttel and Bernhard-Reversat 1975
	6.78	9.04	Huttel and Bernhard-Reversat 1975

Table 1. (continued).

Life Zone[a]	Litterfall Leaf and Fruit (mt/ha.yr)	 Total	Source
	3.06	8.33	Malaisse et al. 1975
	6.18	9.15	Malaisse et al. 1975
	4.69	5.9	Malaisse et al. 1975
	7.04	10.54	Nye 1961
ST-Lower Montane Rain Forest:	2.20	2.42	Dugger 1978
ST-Wet Forest:	5.55	11.65	Kunkel-Westphal and Kunkel 1979
	7.81	9.33	Kunkel-Westphal and Kunkel 1979
	7.73	10.02	Odum 1970
ST-Lower Montane Wet Forest:	5.7	6.5	Tanner cited in Grubb 1977
	5.2	6.6	Tanner cited in Grubb 1977
	5.3	5.5	Tanner cited in Grubb 1977
	4.4	5.5	Tanner cited in Grubb 1977
ST-Moist Forest:	6.16	7.72	Bandhu 1973
		5.48	Dugger 1978
		10.0	Ewel 1976
		9.0	Ewel 1976
		3.16	Singh 1968
		4.20	Singh 1968
		5.02	Singh 1968
		6.20	Singh 1968
	3.64	7.88	Singh 1975
ST-Dry Forest:	4.04	4.82*	Garg and Vyas 1975
	2.0	2.40	Lugo et al. 1978
	2.48	2.88	Lugo et al. 1978
	0.84	1.02	Lugo et al. 1978

* Assumed same ratio of leaf to total litterfall as at other 3 sites (1.19).

[a] T = Tropical, ST = Subtropical.

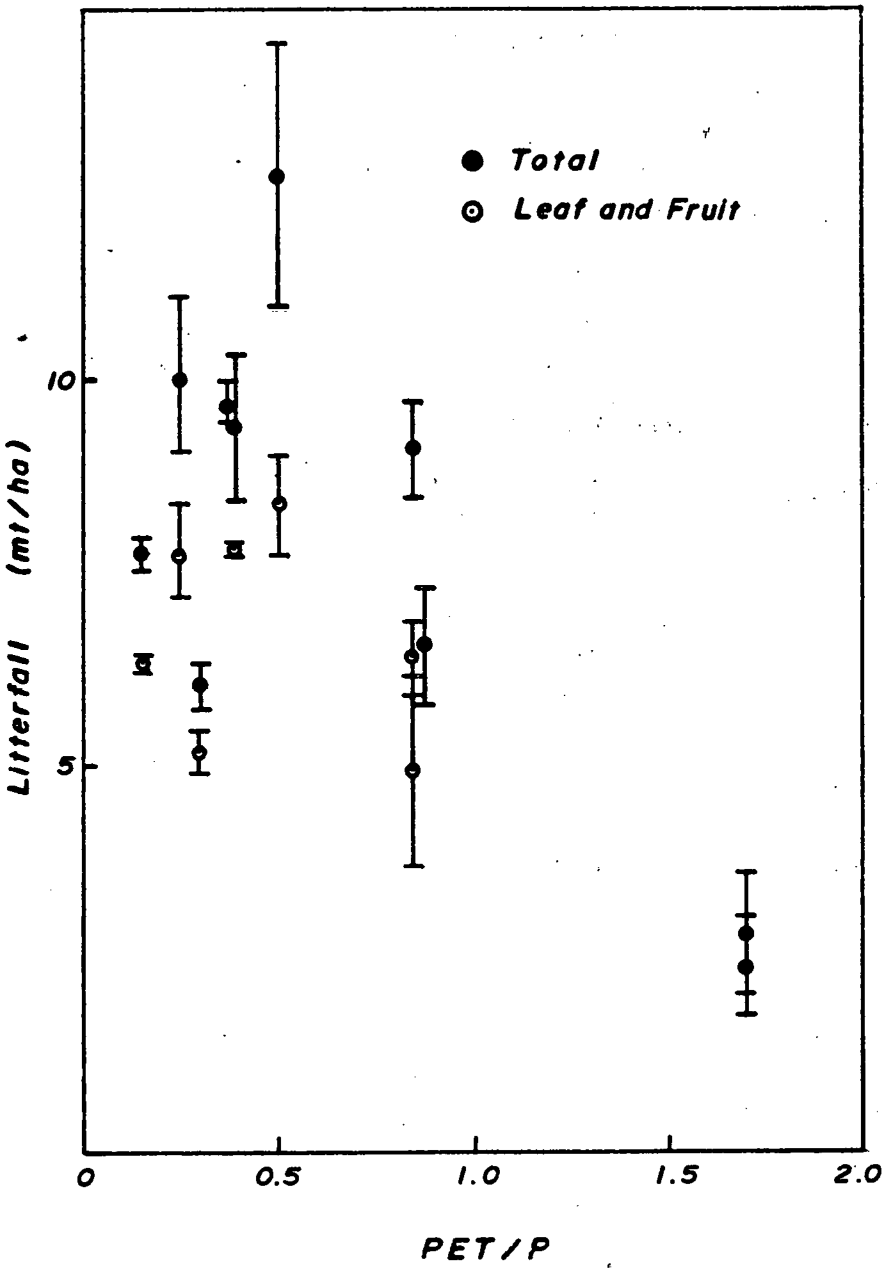

Fig. 9. Relationship between litterfall and potential evapotranspiration to precipitation ratio (PET/P). The points represent the mean litterfall (from Table 1) ± 1 standard error (bars).

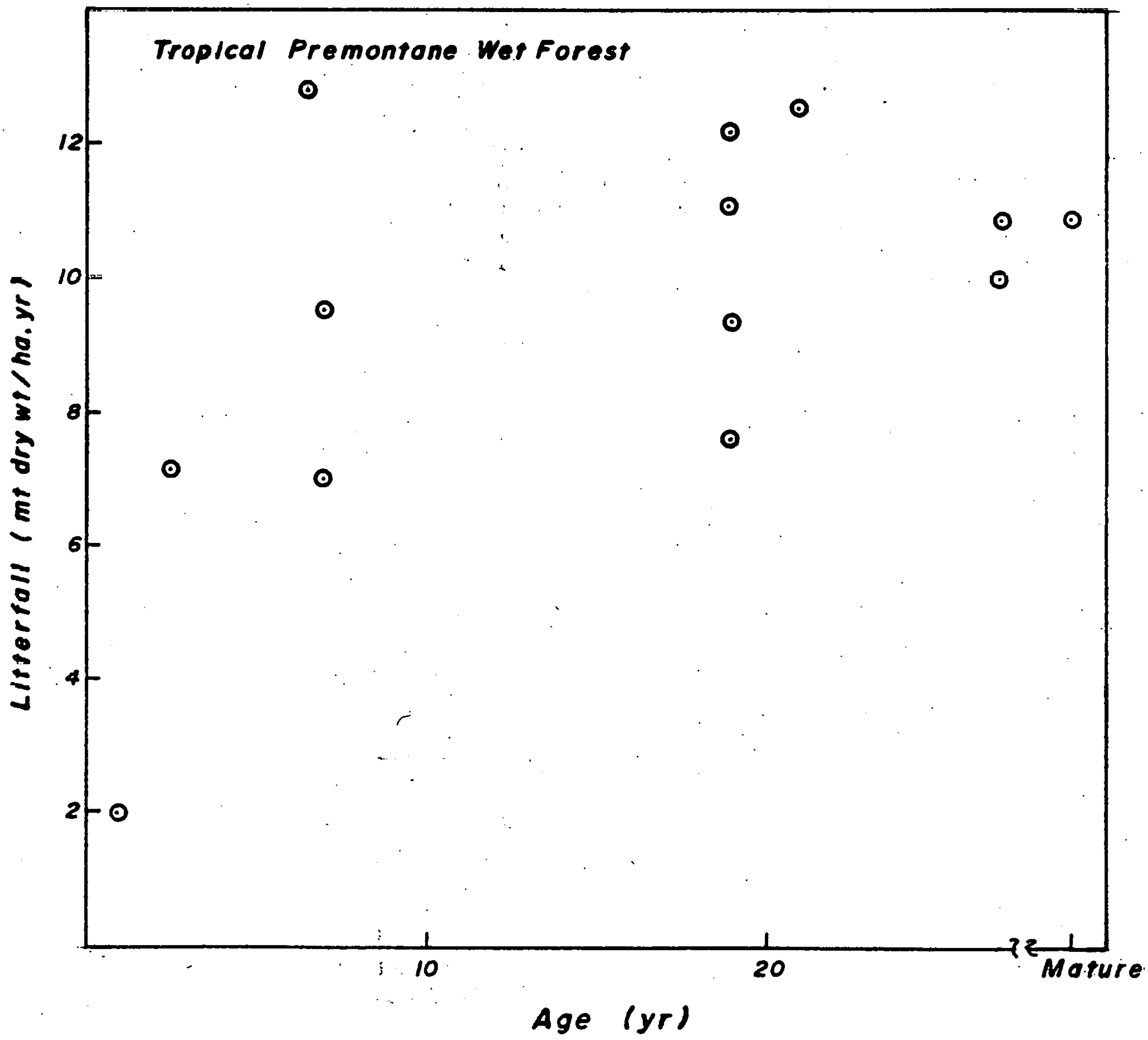

Fig. 10. Relationship between litterfall and stand age in a Tropical Premontane Wet Forest Life Zone (data are from Kellman 1970).

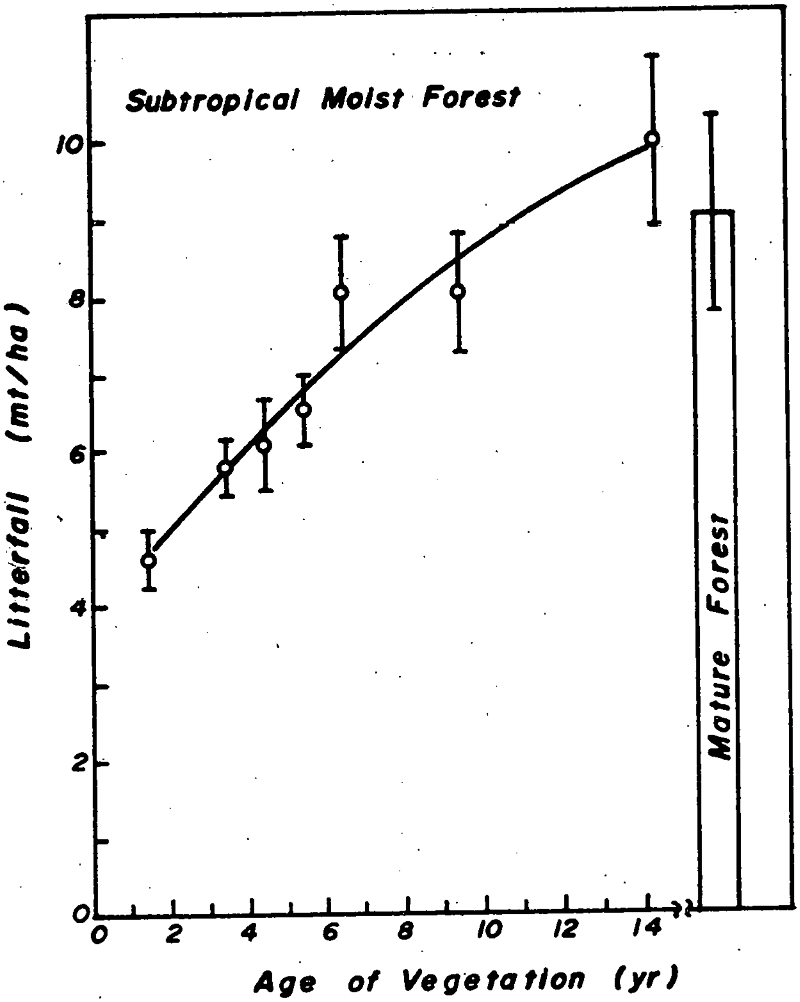

Fig. 11. Relationship between litterfall and stand age in a Subtropical Moist Forest Life Zone (Ewel 1976).

Using the litterfall data in Table 1, grouped into the six Life Zone categories described in the paper by Brown and Lugo (this volume), and the area of the six Life Zone categories, I was able to estimate the annual production of litter for tropical forests (Table 2). Most of the total litter production in the tropics occurs in the Tropical Moist Forest Life Zone (43%), and the least in the Subtropical Rain and Wet Forest Life Zone (4%). Leaf and fruit production account for 76% of the total litter production in the tropics. Brown and Lugo (this volume) estimated the standing crop of litter in the tropics to be 7.1 billion mtC, and using the total litter production from Table 2 (6.04 billion mtC/yr), the turnover time of litter in the tropics is approximately 1.2 yr.

Turnover times for individual Life Zone groupings are summarized in Table 3. The Tropical and Subtropical Dry Forest Life Zones have the longest turnover times, followed by the Tropical Rain and Wet Forest, Tropical Moist Forest, Subtropical Moist Forest, and finally by the Subtropical Rain and Wet Forest. The Dry Forest Life Zones have turnover times on the order of 2 yr, whereas the other Life Zones have turnover times on the order of 1 yr.

Ajtay et al. (1979) estimated a litter production of 11.0 billion mtC/yr for the tropics, and Reiners (1973) estimated a value of 11.4 billion mtC/yr. Both of these estimates are about double that of mine. The main reason for this discrepency is that Ajtay et al. and Reiners use average annual litter production rates that are about 2.0 times and 1.7 times higher, respectively, than the average annual litter production rate that I found. In addition, Ajtay et al. used a lower area (1,480 million ha) for the tropics and Reiners used a higher area (2,000 million ha) than I used.

In summary, large amounts of organic matter turn over in tropical forests every year. The faster the turnover, the higher is the capacity of these forests to capture CO_2 from the atmosphere. Also, there is a better opportunity for the storage or transfer of carbon to other sectors of the biosphere where return to the atmosphere is delayed. Yet, I have only reported on litterfall and biomass accumulation with age. More work is needed in the other components of net primary productivity as well as rates of respiration by ecosystem component.

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Table 2. Estimated litterfall production in tropical forest ecosystems.

Life Zone[a]	Area (10^6 ha)	Litterfall Leaves (mt/ha.yr)	Litterfall Total (mt/ha.yr)	Total Litterfall Leaves[b] (10^9 mt/yr)	Total Litterfall Leaves[b] (10^9 mtC/yr)	Total Litterfall Total[b] (10^9 mt/yr)	Total Litterfall Total[b] (10^9 mtC/yr)
T-Rain and Wet Forest	211.2	6.96	8.82	1.47	0.74	1.86	0.93
T-Moist Forest	472.2	7.21	10.91	3.40	1.70	5.15	2.58
T-Dry Forest	244.5	5.0[c]	5.5[c]	1.22	0.61	1.34	0.67
ST-Rain and Wet Forest	74.3	5.58	6.55	0.41	0.20	0.49	0.24
ST-Moist Forest	283.0	4.90	6.52	1.39	0.70	1.85	0.92
ST-Dry Forest	494.9	2.34	2.78	1.16	0.58	1.38	0.69
TOTAL	1,780			9.15	4.58	12.07	6.04

[a] T = Tropical, ST = Subtropical.

[b] Carbon assumed = 0.5 x dry weight.

[c] Interpolation, by eye, from Fig. 9, using a PET/P = 1 for T-Dry Forests.

Table 3. Estimated turnover time (yr) of litter by Life Zone.

Life Zone[a]	Standing Crop of Litter[b] (10^9mtC)	Total Litter Production[c] (10^9mtC)	Turnover Time (yr)
T-Rain and Wet Forest	1.06	0.93	1.14
T-Moist Forest	2.27	2.58	0.88
T-Dry Forest	1.34	0.67	2.00
ST-Rain and Wet Forest	0.18	0.24	0.75
ST-Moist Forest	0.74	0.92	0.80
ST-Dry Forest	1.48	0.69	2.14
TOTAL	7.1	6.0	1.2

[a] T = Tropical, ST = Subtropical

[b] Product of standing crop per unit area (Table 10 in Brown and Lugo, this volume) and area of Life Zones.

[c] From Table 2.

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THE DEVELOPMENT OF AN EMPIRICALLY-DRIVEN SIMULATION MODEL OF CARBON EXCHANGE BETWEEN HUMAN-IMPACTED TROPICAL ECOSYSTEMS AND THE ATMOSPHERE

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Introduction

One emerging focal point for recent research on the global carbon cycle has been the attempt to assess whether our knowledge of the global carbon cycle can be integrated into a consistent quantitative balance. At the present time there is considerable controversy as to whether tropical terrestrial regions are a source or a sink of carbon with respect to the atmosphere, and carbon research since the Brookhaven symposium has done remarkably little to decrease the conceptual gap between those who view the terrestrial biota as a source vs. a sink of carbon. The conclusion of most recent studies (see Broecker et al. 1979 and Woodwell et al. 1978 for a few of many examples) is that it is not possible at this time to produce a balanced annual carbon cycle unless a new sink is found beyond the atmosphere and the ocean, at least as they are presently assessed. One such possible sink that often is evoked is the land biota (see papers by Lugo and by Holdridge in this volume) especially if it is fertilized substantially by the increasing atmospheric CO_2 concentrations. However, if Woodwell et al. are correct in their assessment of large net additions from terrestrial biomass, such CO_2 fertilization cannot make up for new cutting, and our knowledge of the carbon cycle still remains very much incomplete. If a balanced budget is to be obtained other sinks must be found. Our preliminary quantitative model simulation analysis, developed below, begins the assessment of the sources and sinks of carbon that occur as different lands are used for various purposes (including no management).

This paper also develops several possible pathways by which the "missing carbon" might be "found" without invoking the nearly-impossible-to-quantify mechanism of CO_2 fertilization of standing crop. The focal point for our analysis is the humid tropical ecosystems, and we emphasize here how sinks might operate where source mechanisms have been identified earlier (e.g., Woodwell et al. 1978).

Forested tropical lands store large quantities of carbon as organic matter, both per unit area and for the tropics as a whole (Brown and Lugo, this volume). As people utilize these lands for various economic activities carbon is transferred between the land and the atmosphere and the atmosphere and the land. In our opinion many analyses of the role of terrestrial vegetation are overly simplistic. Clearly many different types of ecosystems, under different management regimes and different environmental perturbations, are likely to be sources of carbon to the atmosphere while other types are sinks. We should move away from the hard positions of the biota as a "source" or a "sink". Rather, we should assess one by one different vegetation types subjected to different patterns of land-use and land-use change. Then the quantitative importance of each type or region can be assessed. Perhaps in the end it is justified to ask what the net effect of the biota as a whole is but such an assessment first requires careful assessment of individual systems.

Possible Role of Forest Recovery and Shifting Cultivation

Our present DOE-funded research, focusing on tropical ecosystems, has led us to questions about "slash and burn" agriculture (also called "shifting cultivation" or "swidden") and other agricultural activities. Our view has been strongly enhanced by the manuscript by Seiler and Crutzen (1980) and by our review of Bolin et al.'s (1979) "The Global Carbon Cycle" (Hall and Detwiler 1980).

Our earlier unpublished simulation suggested that some large portions of the terrestrial vegetation might serve as a sink for carbon even though that vegetation was subject to cutting if 1) the vegetation recovers substantially, and 2) a substantial portion of the vegetation cut is stored as some kind of slowly degrading product, such as lumber. Under this scenario (which we analyzed quantitatively via simulation) the forest system would be in long-term balance (more or less) while a certain fraction was removed to storage resulting in a net movement of carbon from atmosphere to storage. Our subsequent research has shown that it is unlikely that lumber is removed from tropical forests at a rate sufficient to account for the "missing carbon" (Lugo, this volume). However, our intervening work, plus informal communications with Steve Schneider of NCAR, and our detailed examination of the manuscript by Seiler and Crutzen (1980), has convinced us that it is possible for the general scheme we developed earlier to operate in tropical forests if we include the provision that the carbon is stored on site (in various slowly-degrading products of cutting and/or combustion) or lost in "natural" flows from the site (such as in groundwater or stream flow).

We believe the principal slowly-degrading pathways to be: 1) the boles left onsite, 2) charcoal left from burning, and 3) "soot" that becomes airborne upon burning and that falls to earth at other locations. Consider a large area in steady state with respect to swidden agriculture over a large number of years, e. g., a 1,000 ha region in which 50 ha are cut each year, farmed for 2 yr, and allowed to lie in fallow for 18 yr, with no change in human population or per capita land use over a century. Under these circumstances, and if the vegetation on the site recovers fully in 18 yr, there would be no year-to-year change in the living (including litter and, presumably, soil) carbon on site. However, if there is any carbon that accumulates in any way, either on site or off, as a function of the land-use (swidden), that carbon would have been a net movement from the atmosphere to that storage. Seiler and Crutzen (1980) suggest that only 15-30% of the carbon on most swidden sites exposed to fire actually burns. Nearly all photographs that we have seen of swidden sites show large numbers of standing dead boles in areas that are actively cultivated. Clearly large quantities of charcoal are left on site. All investigators that we have talked to who have visited swidden sites (Risch in Mexico, Farnworth in Venezuela, Ewel in many countries) have told us that large quantities of charcoal remain on the ground. Ewel hazarded a guess that 5-10% of the original biomass remained as charcoal (not counting that part of the boles, etc. that was not charred). Farnworth and others report layers of charcoal in soil pits dug in supposedly virgin Amazonian forest. It is not necessary for the carbon to remain on the surface, for trampling by farmers and partial decomposition could produce charcoal fines that would enter the soil and even be carried away in surface or groundwater. Presumably the charcoal decays only very slowly. Additionally, large quantities of slowly degrading materials could leave an active swidden site in soot from fires and in relatively fine particulate carbon lost from the soil surface when it rains.

As we continue to investigate how different land-use changes, and different vegetation types associated with shifting cultivation, would result in different net exchanges of carbon with the atmosphere, it will be useful to identify and contact historians of tropical countries to investigate what sort of data bases might be available for quantitative land-use estimates over time, and then to simulate these patterns. In the meantime we have gathered about two dozen references that provide quantitative information on shifting cultivation (e. g. Cowgill 1961, Kans and Moorman 1977, Manshard 1968, Newton 1960, Watters 1971, Williams and Joseph 1973).

Soluble and Particulate Carbon Fluxes in Natural Ecosystems

Likens and MacDowell (1980 personal communication) reported results of investigations of soluble and particulate carbon flux in the Hubbard Brook Experimental Forest, New Hampshire. There were surprisingly large carbon fluxes associated with the influx, throughfall, and percolation of rainwater. About 1.0+ ppm carbon was associated with the infalling rain, equivalent to an input of about 10-30 kg/ha.yr. This concentration was increased by a factor of about 10 as the water fell through the trees, picking up organics from the vegetation. Soil water near the surface of the soil had even higher concentrations, as much as 50 ppm. But, concentrations were reduced to about 3 ppm beneath the C soil horizon, indicating that the majority of this carbon was somehow filtered out in the mineral portions of the soil or respired by microbes. Movement of carbon through other forested watersheds was described by Lugo (this volume). In addition, we propose that acid rain could be leaching carbon from the leaves at a rate greater than the historical mean and sequestering carbon in the lower soil layers more rapidly than it is/was decomposed. Worldwide this might constitute a sink of considerable magnitude although much of the leachate is probable labile. While little data are to our knowledge available on this question for tropical systems, we wondered whether new carbon might be brought into tropical systems from atmospheric sources, perhaps particularly as charred material from other burning sites. This material could eventually be sequestered in the soil, along with other refractory materials such as small particles of charcoal and, perhaps, acid-produced leachate, adding to this potential sink. Although the question is most properly investigated empirically and on site, certain aspects are amenable to analysis with our existing model.

The Use of Models

Since the processes contributing to land-use changes and to what happens to carbon once stored as living biomass are very complex, and since "tropical forests" encompass so many different types of landscapes (ecosystems, Life Zones), each subject to many different sorts of land-uses, the problem becomes quickly much too complicated to deal with using conventional algebra. Clearly some sort of computer model is necessary, one that can do the very large amount of bookkeeping involved, make projections readily from the past and into the future, and explore through sensitivity analysis the importance of concepts and parameters that are not known well.

Many possible models of forest growth and land-use change are available in the literature. However, we did not find any of these appropriate to our problem of simulating carbon-exchange in the tropics. The principal reason is that there is essentially no known set of equations that can adequately and mechanistically represent the factors that determine the rates and quantities of tree growth and death and decay such that they could be extrapolated to the level of forests that do not have very comprehensive data sets. Therefore our approach to modeling tree growth, and virtually all other components of the carbon inventory and exchange system, is to start with the most straightforward, empirically-determined components and construct our simulation from there. Although this approach has the limitations of any model that does not include mechanistic components of cause and effect, it does have the virtue of not pretending to model beyond the (rather limited) data set that we do have.

Our first step was to determine from the literature what sort of information was available and how this could be applied to the carbon question. Our conclusion was that there was almost no information that could be applied at the level of the forest ecosystem except for measurements of carbon stored-on-site and land-use data. For example, virtually all flux rates in the literature were derived as rates of change of biomass rather than as an independent (e.g. gas exchange) estimate of flux. For another example, rates of change of land-use were rarely obtainable as rates per se but more characteristically as differences between estimates at several points in time. Therefore we developed a model structure that was based on these obtainable data types. We believe it is sufficient to answer many questions about carbon in the tropics. Due to the characteristics of the data base our overall strategy was to construct a model that would read in appropriate raw data as quantities at points in time, generate various annual rates of change from that data, and then inventory the carbon on all land-use regions. Differences between such total inventories from one year to the next were assumed to represent exchanges with the atmosphere.

For most of the data available on both biomass and land-use there was rarely more than two or at the most three data points available (for example, quantity of land in "permanent" agriculture in 1950 and 1975). Since there was often little further information about the interconnecting points between these known two or three points we developed a generalized function (GENFUN I) that allows any two data points to be connected by a straight line or by curves of increasing or decreasing magnitude (Fig. 1a). A family of all such curves defines essentially all "regular" ways that one can get from A or B. Where three or more points are known a single curve can, of course, be defined. For all possibilities sensitivity analysis can be used to determine the importance of the curve shape for whatever conclusions might be reached with the model. We also have developed a more sophisticated curve-fitting procedure (GENFUN II) but have not used it yet (Fig. 1b).

Data Requirements

The principal variables that were thought to be most important to the question of net exchange between forested areas and the atmosphere, and that will explicitly be simulated for best-estimate and maximum possible values, follow. Each question requires the following information for a specific Life Zone, nation or region, depending on the scale of the question asked. Eventually we hope to run <u>all Life Zones</u> for <u>all</u> nations <u>in</u> the tropics. The data required are:

- the rate at which both virgin and secondary forest is cut, the change in this rate over time, and the use of these cleared areas;
- the fate of the harvested biomass - how much went into long-term storage (e.g. lumber or charcoal or slowly decomposing boles) versus how much was quickly (1 year) oxidized (e.g. burned wood, small pieces of harvesting residue, twigs, and leaves);
- the biomass of both virgin and second-growth forests after they have reached their maximum size;
- the length of time required for cut areas to regain original, or at least the new maximum biomass;
- the pattern of forest regrowth (e.g. linear, logistic, etc.);
- the age at which, on average, the plot is cut again if it is cut again;
- an assumption (yes or no) about the possibility of carbon dioxide fertilization effecting productivity and storage of carbon in both regrowing and mature areas (not operational yet);
- the mean decay rates of different refractory material types, i.e. boles, charcoal, soot, etc. (not operational yet). We do not need the rate, only the points in time, the program calculates the rates;
- the possible patterns of historical rates of land-use change.

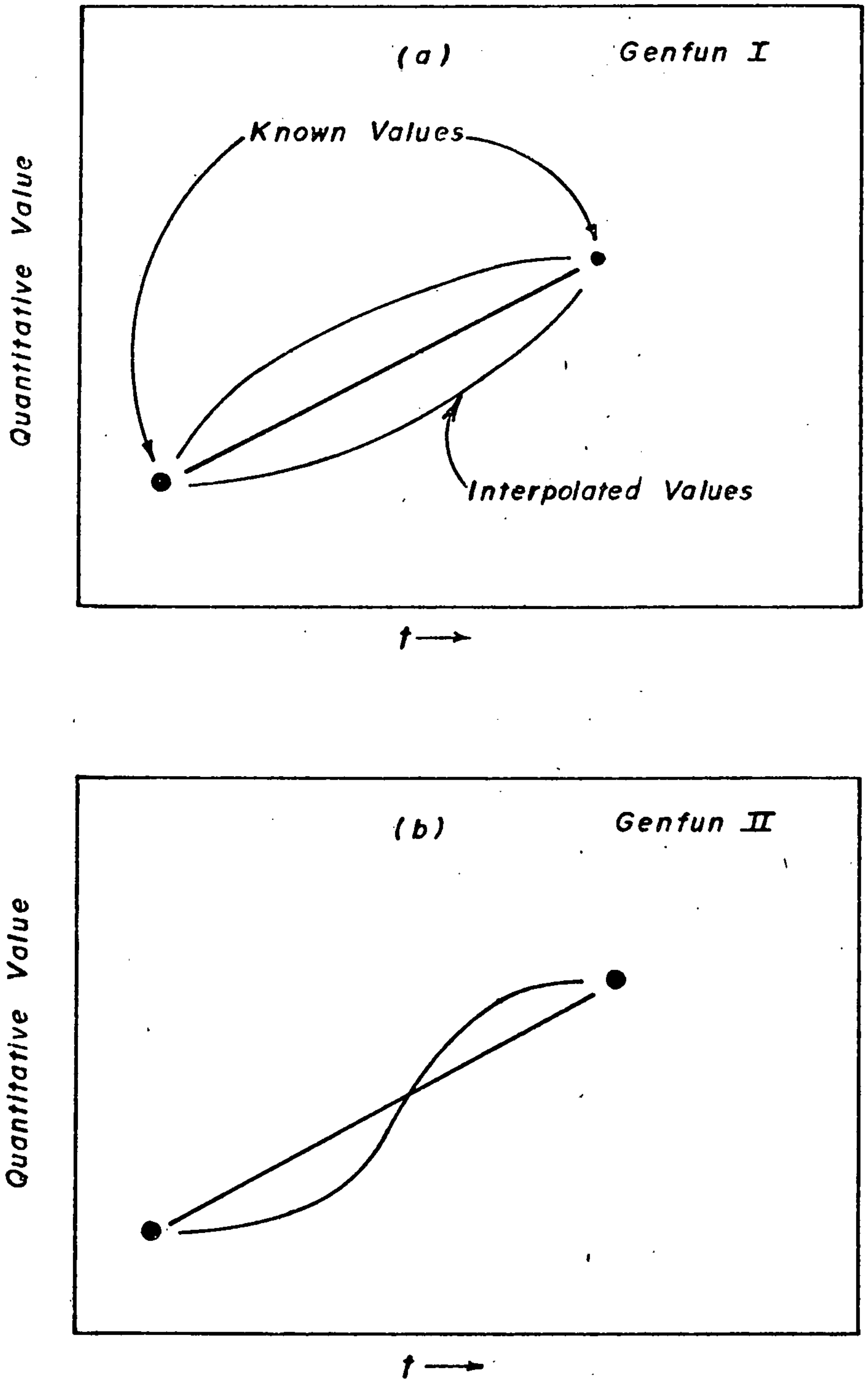

Fig. 1. GENFUN I and GENFUN II with different second derivitives.

Other components of our project are deriving this needed information for selected tropical regions (see papers by Brown, Brown and Lugo, and by Tosi in this volume).

The next problem was to define the types of land-use that were particularly important either in terms of carbon standing crop, intensity of land-use changes or potential for sequestering large quantities of carbon. In addition, it was important to define as few land-use areas as possible consistent with the above criteria to decrease the types of data required, and to make each clearly differentiated by, e.g., remote sensing. In other words we wanted to make a model that depended as much as possible on data bases that we thought are available, or might become available. A more sophisticated model might be useful for some questions but would not be useful if it asked for data that were unobtainable.

A General Pattern of Land-Use in the Tropics

Almost all existing assessments of the role of the tropical biota in the global carbon cycle are essentially "one box" models that have the biota responding to external forcing functions such as changes in the concentration of CO_2 in the atmosphere and/or human forest-cutting rates. Our discussions with people familiar with patterns of land-use in the tropics, and such references as we have so far been able to locate indicate that the pattern of land-use change is much more complex than existing models represent, but that such land-use changes do tend to follow certain patterns.

In general, virgin forests are not managed in ways that result in large changes in biomass. For example, mahogany or fruits may be harvested from such forests, but as long as the region remains essentially uncleared the remaining vegetation, stimulated by sunlight entering through the gaps created in the canopy, quickly grows in to fill any gaps with presumably little net exchange of carbon with the atmosphere.

The first stage in human land-use change tends to be the introduction of shifting cultivators, often following the development of logging or other new roads (Watters 1971). For example, as much as 50% of potentially cultivatable land in Mexico had been "lost" to shifting cultivators by 1945 before other major land-uses were introduced. Virgin forest cutting for shifting cultivation becomes more intense in the region as other settlers follow the roads, although the farmers prefer, in general, to cut second growth regions (which are easier to fell) than virgin timber (Watters 1971). It is uncommon for shifting cultivators to return to a stand more than 20 yr-old (Watters 1971). If, and as the land is used more intensively, following e.g. population increases due to settlement of additional people or through reproduction, and/or through capital investment, and/or decline in shifting cultivation fertility, land often is cleared and not allowed to grow back (Nelson 1973). Again the easiest, and apparently most common procedure, is to take land already cleared for shifting cultivation (either a recently farmed plot or a second growth plot) and convert the land into other land-uses, specifically permanent agriculture, grazing or "urban" regions. Our current information is that the most important general pathway is from virgin forest through shifting cultivation to a mosaic of grazing-small scale permanent agriculture-abandoned but degraded land, each of which has carbon storages roughly similar (Coulter 1972, Nelson 1973). Another, probably less quantitatively important, pathway is capital intensive land clearing such as the Jari project in the Amazon, or the Brazilian government-endorsed project of developing strings of agricultural villages throughout the Amazon (Goodland and Irwin 1974). In this case, virgin forest is cleared completely and converted directly to farming or tree plantations or some other land-use. Finally, abandonment of uneconomic land is an important land-use change. It is important that a computer model assessing carbon inventories reflects these principal patterns of land-use change. Figure 2 is our final conception, arrived at after many revisions, as to what land-use classes and changes in land-use might best represent (in the computer) fundamental components of the carbon question. A slight revision incorporating changes suggested at the Rio Piedras symposium is being developed. The flow chart represents land areas in each category, and the arrows represent the transfer of land area from one category to another. The land-use categories and their reason for inclusion are:

1) Natural systems (AREANS in the program) -- included because it is thought that when a given region, Life Zone, nation, etc. was undisturbed it is assumed that all land would be in this category with a biomass of carbon similar to surviving representations of this vegetation. If the land is disturbed it will "enter" (in the model area will be transfered to) one of the following land-uses and the area in the natural system category will be diminished by that amount.

2) Area cleared for shifting cultivation (AREASB1, AREASB2) -- probably the single largest category of land cleared in a given year, at least historically. This land-use results in plots of low living-carbon inventories that are farmed for about two years and then allowed to go to fallow or are used more intensively (e.g. pasture).

3) Regrowing or fallow areas (AREARG) -- once a swidden plot is abandoned the living carbon inventory on the site will accumulate if the plot is not disturbed. The land-use in the model moves year by year through successive categories of recovery, each characterized by a specific quantity of living (and dead) carbon that can be represented through the use of our "GENFUN" routine. Land is removed from the fallow cycle once vegetation has recovered according to a predetermined "optimal regrowth period" (say 15 yr) except as modified by demand for new farmland. In other words, if the number of farmers (or the land they use) remains constant from year to year then the quantity of land leaving the "15 yr-old category" will be equivalent to the amount of land entering the fallow period and the quantity of land moved from each regrowing category to the next (say the 7th yr of fallow to the 8th). If, however, the quantity of land farmed increases then all of the 15th yr of fallow will be cut as well as some of the 14th. Over time new land will come from successively younger fallow plots (Watters 1971) unless new land is cut from virgin forest (a user option). If less land is cut for farming over time, land will be allowed to enter longer periods of regrowth and mature second-growth forest will accumulate.

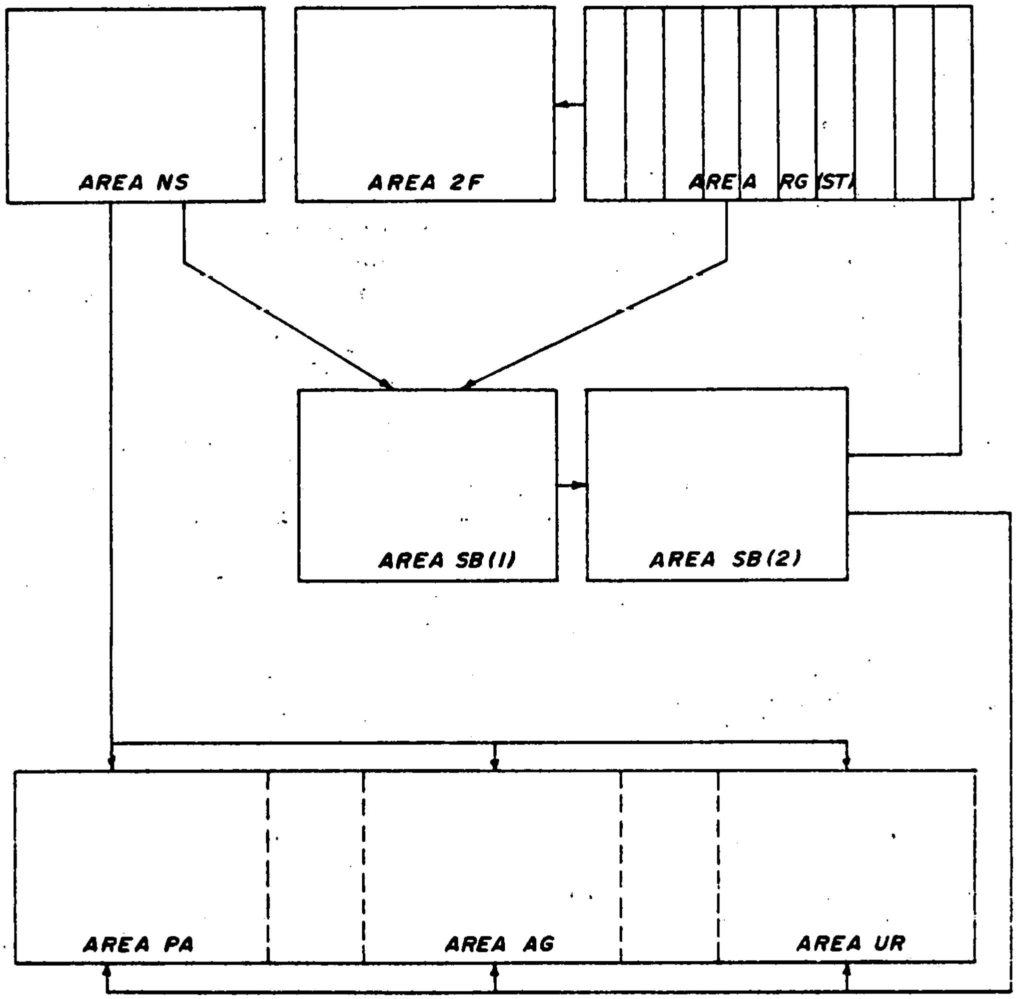

Fig. 2. Land-use flow chart for the model GLOBC4. See text for meaning of mneumonics. Boxes indicate area of land in various land-use categories. Finely divided box at upper right indicates different stages of forest recovery. Arrows indicate pathways of land-use transition in the present model. AREAPA, AREAAG and AREAUR were combined for the preliminary runs as the biomass is similar.

4) Area used for intensive human activities -- land cut for swidden can also be converted to other land-uses such as pastures (AREAPA), urban land (AREAUR), or permanent agriculture (AREAAG). This is an option that can be entered into the model by the user at the start of a run. The importance of this pathway derives from the observation that the principal way that land is moved into intensive use (e.g. urban, pastures, and/or permanent agriculture) is through the intensification of activity on land initially utilized for shifting cultivation.

Derivation of Basic Parameters for Test-Case Run

It is not possible at this time to run our model for any real countries, Life Zones or other land units. As time goes on this information will be available for an increasing number of specific Life Zones and countries, since other members of our research group are gathering much of this needed information and additional data on land-use changes will be available as remote sensing is applied to the problem.

However, we are able to construct at this time a basic data set that appears not unrealistic and that can be used to explore what are important components of needed information and the kinds of answers we might eventually expect. We chose the moist tropical forests of Latin America as our test region because some of the needed information was available for that region and because land-use changes in that region appear important to the basic carbon question.

The land area of 803 million ha was determined from Sommer (1976) who estimated that this area represents the original area of tropical moist and wet forests in Latin America. The biomass of virgin regions of these forests was estimated as about 200 mtC/ha, consistent with values in Whittaker and Likens (1973) and slightly higher than our own more recent analysis (Brown and Lugo, this volume). Land in shifting cultivation was estimated as about 52 million ha (Seiler and Crutzen 1980, Watters 1970). We have assumed that all shifting cultivation in Latin America is in the moist and wet forest types which probably overestimates slightly the total proportion of moist and wet forests that is in shifting cultivation. We assumed that the fallow cycle is 15 yr (from values given in Ruthenberg 1976) and we assume that new land is cleared for shifting cultivation at the rate of about 3.5 million ha/yr, a figure originally determined from the total land area in cultivation and the length of the fallow cycle.

Preliminary Results of Model Simulations

We have used our present-generation model (GLOBC4) to explore some scenarios of land-atmosphere carbon exchange, using what we think are not-unrealistic assumptions about land-use changes. Since the results of this model are completely sensitive to the land-use and biomass data used as input it is important to derive these parameters as explicitly as possible. Then the model can be used to test the significance of the data base to the carbon question and, alternately, to test the importance of poorly known components of the data base.

The results of these preliminary runs are summarized in Table 1. At this time it is important to emphasize that the runs are not a real assessment of what we believe are actual carbon exchange rates, but rather scenarios as to what the carbon exchange would be if certain land-use changes in fact took place over the 50-yr period 1930-1980.

The accuracy of the present model's output in reflecting what actually is taking place is a function of the accuracy of our on-site carbon estimates, which we think are fairly good for above ground carbon. It is also a function of the accuracy of our estimated rates of land-use changes and at present these are known only very poorly. However, even the present data set and model allows an examination of what the range of carbon exchanges are likely to be if the rates of land-use change are similar to the literature values and assumptions that we presently are using. The Latin America results can be, in a sense, extrapolated to the tropics in general by multiplying the numbers in Table 1 by 2.5, since Latin American forests contain about 40% of the carbon in all tropical forests. We recognize that these kinds of extrapolations are dangerous but they are done simply to compare our preliminary results with those of others.

The results of these preliminary runs suggest that it is most likely that the tropics will be a source of carbon to the atmosphere, but that it is unlikely that they will be a source as large as the higher numbers given in Woodwell et al. (1978). We have not yet added the carbon export pathways suggested by Holdridge and by Lugo (this volume) to the model which may reduce the magnitude of this carbon source further. Our conclusion of no large net source is most importantly sensitive to our assumption that a large percentage (i.e. more than about 40%) of land that is cut in the tropics is left to grow back to some kind of moderate-stature vegetation, in one form or another, and that gross cutting rates do not greatly exceed about 1.8%/yr. With these assumptions we find that during this simulated 50-yr period there tends to be a net loss of carbon from Latin American tropical forests on the order of 0.2 to 0.6 billion metric tons (BMT)/yr, or, extrapolating to all tropics, 0.5 to 1.5 BMT/yr. Under some assumptions they were a small sink (Run 2). And, we were unable to produce very large sources.

The present model does show some interesting behavior with respect to first derivatives, but not second derivatives, of land-use change. For example, even if virgin land is cut for swidden for all years during the 50-yr period the contribution of that landscape to the CO_2 changes in the atmosphere observed during 1958-1980 (the period of atmospheric record) can be influenced only slightly by whether the rate of cutting is increasing or decreasing (Runs 1 and 2). Larger second derivatives may make the change in rate of cutting more important. Assuming that the rate of increase of cutting virgin forests had a very large negative inflection (the lower curve in Fig. 1a) then the quantity of carbon added during the period of atmospheric record would be very large per year. If, on the other hand, the cutting rates, even if high, were slowing down, there could be absorption of carbon by this biota. This type of response occurs both with respect to the rates of land-use changes from natural systems to swidden (or other land-uses that allow regrowth) or by increasing/decreasing the rate of cutting within the swidden cycle itself.

During all runs any accumulation of carbon on the swidden sites was moderated by land-use changes that shifted land to higher intensity use, such as pasture (Run 4).

Table 1. Preliminary model (GLOBC4) results for tropical wet and moist forest in Tropical Latin America. (Total area = 803 million ha).

RUN		Cutting rate	Land Use[a]								Carbon Net Exchange			
			AREANS[b]		AREASB (1+2)		AREARG		AREAPA[c]		Total from 1930 to 1980		Mean per year, 1958 to 1980	
			1930	1980	1930	1980	1930	1980	1930	1980	Linear[c]	Range	Linear[d]	Range
		(%/yr)	(10^6ha/yr)								(10^9mtC)			
GLOBC4-	1a	0.3–0.9	761	761	5.0	14.9	37.5	27.6	0.0	0.0	-	-1.45	-	-0.016
swidden area increases	1b					same					-1.45	to	-0.016	to
	1c					same					-	-1.45	-	-0.016
GLOBC4-	2a	0.9–0.3	675	675	15.0	5.1	112.5[b]	77.5	0.0	0.0	-	+9.14	-	+0.24
swidden area decreases	2b					same					+9.16	to	+0.24	to
	2c					same					-	+9.18	-	+0.24
GLOBC4-	3a	0.9	718	629	10.0	15.0	75	75	0.0	88.0	-	-16.75	-	-0.52
swidden constant transfer of	3b					same					-16.56	to	-0.52	to
land from natural to pasture through swidden	3c					same					-	-16.35	-	-0.56
GLOBC4-	4a	1.1	712	536	15.0	15.0	75	75	0.0	176	-	-33.45	-	-0.69
same as above but	4b					same					-33.26	to	-0.66	to
additional direct transfer from natural to pasture	4c					same					-	-33.05	-	-0.66

[a] AREANS = area of natural systems
AREASB = area of shifting cultivation
AREARG = area of regrowth
AREAPA = area of pasture

[b] Includes recovered second-growth; 26 x 10^6 ha older than 15 yr

[c] Includes pasture, permanent agriculture and urbanized land

[d] linear (case b) means GENFUN I 2nd derivative = 0, range is with positive (a) and negative (b) 2nd derivatives of 0.05

The values in Table 1 are likely to be diminished (for these assumptions) in our next generation of models because they will incorporate a delayed decomposition component that will release carbon left from incomplete combustion or utilized forestry remnants.

Discussion

Although it is too early for us to assess whether the preliminary results of Table 1 will be close to our final best estimates, they are in agreement with our interpretation of the results from other studies, specifically, the land-use change assessment of Hampicke (1979, see also Hall and Detwiler 1980) and of Seiler and Crutzen (1980) as well as our interpretation of the data presented in Stuiver (1978). None of these values are in agreement with contentions that the land is a sink of more than 1 BMT, or the larger source estimates (4 to 18 BMT/yr) provided by Woodwell et al. (1978). However, we have found that it is possible for us at this time to run our model with values that are not unrealistic and that produce results that cover much of the range given by various groups in the literature. Future research should increasingly narrow the range of values that are most likely. Unfortunately, our analysis is very sensitive to past land-use patterns, and it may be difficult to determine what such patterns were.

We believe that Hampicke's analysis is the most accurate published values presently available because he appeared to devote considerable effort to determining fluxes of carbon from both land to atmosphere and the converse, so that net values could be assessed. His best estimates of from a small source (1 BMT/yr) to a somewhat larger source (up to 2 or an extreme of 4 BMT/yr) is in agreement with our preliminary results (Table 1) and with the assessment of Seiler and Crutzen that the annual net exchange is most likely to be from a 2 BMT source to a 2 BMT sink. When we add later our decomposition function the net exchanges of Table 1 are likely to be somewhat lower.

It is interesting to compare the results of these "bookkeeping" analyses with another independent analysis, that of the change in the ratio of ^{13}C to ^{12}C in the atmosphere. Stuiver (1978) has analyzed these ratios in the rings of trees, since presumably the carbon in the atmosphere in earlier times leaves a record of carbon isotope ratios in the carbon stored in the tree rings. Since living trees discriminate against ^{13}C relative to ^{12}C, any net exchange of carbon from the biota to the atmosphere will change the ratio of ^{13}C to ^{12}C in the atmosphere. Stuiver found a decrease in this ratio during the period of 1880-1950 or so which he attributed to the clearing of forests in North America and elsewhere. He also concluded that this dilution was not still taking place, based on a cessation in the reduction of the isotope level as plotted in his figure 3 (reproduced here as Fig. 3). We interpret this figure differently, for the cessation effect can instead be seen as an artifact of the inter-tree calibration of that figure. Each tree, analyzed by itself, shows a pattern that appears roughly similar (to our eyes) to the data from the 1880-1920 period. In addition, 5 of the 7 trees plotted independently in his figure 2 (Fig. 3) show a continued ^{13}C dilution effect that we interpret as a continuation of the addition of carbon to the atmosphere; i.e. a net reduction of the earth's biota. It may be that our interpretation of Stuiver's data is in error (some trees plotted still need to be corrected

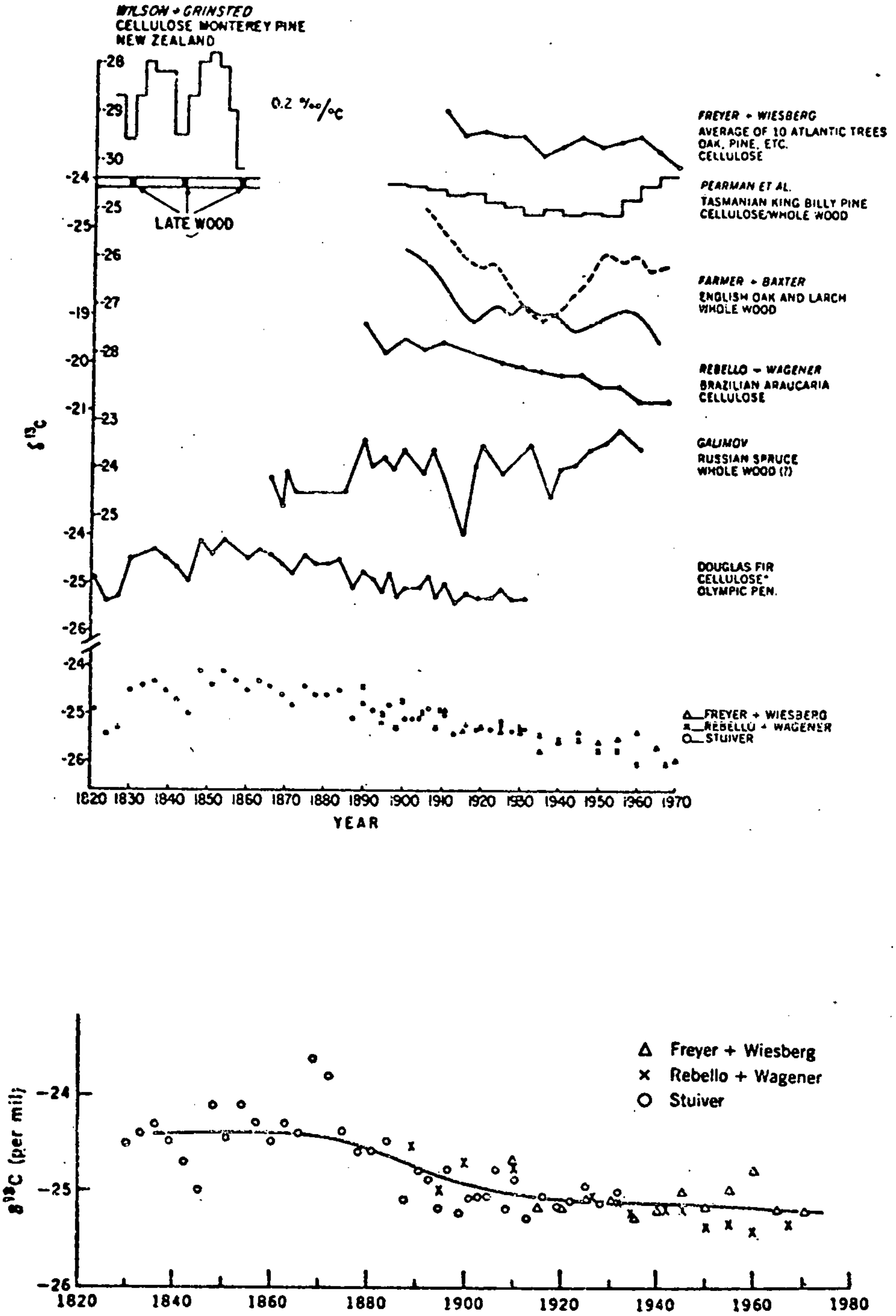

Fig. 3. Record of $\delta^{13}C$ in trees from various regions (top) and change in atmospheric $\delta^{13}C$ after correction for fossil fuel addition (bottom) (Stuiver 1978).

for the industrial source effect). If it is not, then his data is consistent with other studies including our own that suggest that the vegetation of the tropics is probably still making a relatively small contribution to the increase of carbon dioxide in the atmosphere, and that his contribution may be balanced in part by a net regrowth in the industrialized nations, at least as long as oil is relatively plentiful. If the biota is found to be at least not a sink, or perhaps a source, it will still be necessary to find a repository for the "missing carbon". We await further research to complete the latitude 50-80°S portion of Broecker et al's (1979) figure 5 (reproduced as Fig. 4) to see if those data, or data from the Pacific Ocean, show any behavior similar to those of 80°N on that graph (Fig. 4). Additionally, we await further comment from oceanographers in response to Wagener's (1979) suggestion that the ocean carbonate system may be more effective than Broecker et al. and others assume.

In conclusion we emphasize the very tentative nature of our results and conclusions, and that as more data are made available in a format compatible with our computer requirements other conclusions are possible. If that is the case we will have to explain why our results are at variance with the other studies that we have presented here.

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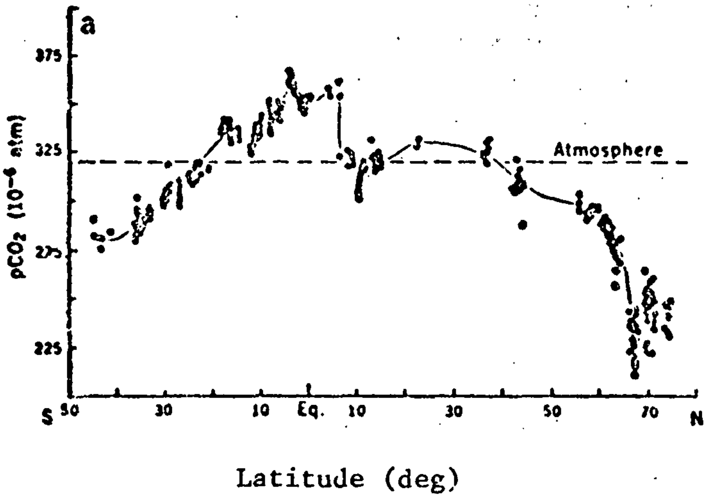

Fig. 4. Partial pressure of CO_2 (pCO_2) exerted by the surface ocean water and that in in the marine atmosphere along the GEOSECS tracks: the Atlantic western basin data obtained between August 1972 and January 1973. The equatorial areas of the ocean give up CO_2 to the atmosphere, whereas the North Atlantic is a strong sink for CO_2 (from Broecker et al. 1979).

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