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# Tropical secondary forests

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ABSTRACT. The literature on tropical secondary forests, defined as those resulting from human disturbance (e.g. logged forests and forest fallows), is reviewed to address questions related to their extent, rates of formation, ecological characteristics, values and uses to humans, and potential for management. Secondary forests are extensive in the tropics, accounting for about 40% of the total forest area and their rates of formation are about 9 million ha $yr^{-1}$. Geographical differences in the extent, rates of formation and types of forest being converted exist.

Secondary forests appear to accumulate woody plant species at a relatively rapid rate but the mechanisms involved are complex and no clear pattern emerged. Compared to mature forests, the structure of secondary forest vegetation is simple, although age, climate and soil type are modifying factors. Biomass accumulates rapidly in secondary forests, up to 100 t $ha^{-1}$ during the first 15 yr or so, but history of disturbance may modify this trend. Like biomass, high rates of litter production are established relatively quickly, up to 12–13 t $ha^{-1}$ $yr^{-1}$ by age 12–15 yr. And, in younger secondary forests (< 20 yr), litter production is a higher fraction of the net primary productivity than stemwood biomass production. More organic matter is produced and transferred to the soil in younger secondary forests than is stored in above-ground vegetation. The impact of this on soil organic matter is significant and explains why the recovery of organic matter in the soil under secondary forests is relatively fast (50 yr or so). Nutrients are accumulated rapidly in secondary vegetation, and are returned quickly by litterfall and decomposition for uptake by roots.

We propose a model of the gains and losses, yields and costs, and benefits and tradeoffs to people from the current land-use changes occurring in the tropics. When the conversion of forest lands to secondary forests and agriculture is too fast or land-use stages are skipped, society loses goods and services. To avoid such a loss, we advocate management of tropical forest lands within a landscape perspective, a possibility in the tropics because land tenures and development projects are often large.

## INTRODUCTION

'*... the majority being exceedingly fast-growing, short-lived, soft-wooded trees of little or no timber value.*' (Richards 1955).

'*... dominated by only a few species of fast-growing pioneers, and these develop into high-volume successional forest that yields a relatively uniform raw material ... forest utilization is still easier when the raw material is relatively uniform.*' (Ewel 1979).

These two statements reflect the change in perception about the use of secondary forests that has taken place in the last 25 yr among experts in the field of tropical forestry. As the area of secondary forests increases, generally at the cost of primary forests, it will be the secondary forests that will have to be managed and used in the future (Ewel 1979). Gómez-Pompa & Vásquez-Yanes (1974) refer to the present as the 'era of secondary vegetation' because, with few exceptions, most tropical countries have larger areas of secondary forests than primary ones.

The literature on tropical secondary forests is scattered and overlaps greatly with that on tropical forest succession. This review is not one on tropical succession, of which there have been several of late (Bazzaz & Pickett 1980, Denslow 1987, Ewel, 1980, 1983), but rather focuses on tropical secondary forests created by human activity. Secondary forests cover large portions of the land area in the tropics (more than 600 million ha; Figure 1) and they are often disregarded by managers and the public as useless brush. This review will

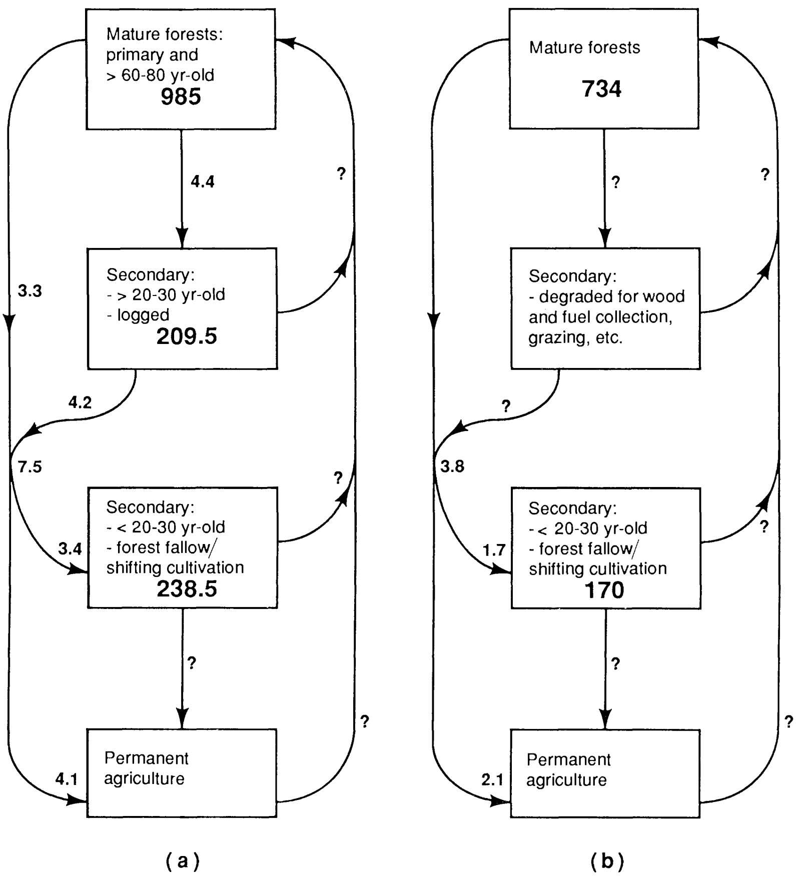


Figure 1. Estimates of forest areas ($10^6$ ha as of 1980) and rates of conversion ($10^6$ ha $yr^{-1}$; 1981–85) of tropical forests to secondary forests (logged and forest fallow) and agriculture for (a) all closed forests lands and (b) open forest lands (data are from Lanly 1982).

address the following questions: what are secondary forests and what human actions create them, what is their areal extent and rate of formation, what are their ecological characteristics, what can they be used for, and what opportunities are there for managing them?

## DEFINITION OF SECONDARY FORESTS

For the purposes of this review, we define secondary forests as those formed as a consequence of human impact on forest lands. We do not include plantation forests which we have already reviewed (Lugo *et al.* 1988). This definition excludes secondary forests resulting from natural disturbances such as landslides, natural fires, and hurricanes. Our emphasis in this review is on secondary forests resulting from abandonment of cleared forest lands generally from agriculture. The types of agricultural practices preceding secondary forests include shifting cultivation (slash and burn) with long or short cultivation periods (about 1 yr to longer than 3 yr) and small or large clearings (less than one to several ha) to 'permanent' agriculture such as pastures or sugar and coffee plantations. Secondary forests (or forest fallows) are an important component of the shifting cultivation cycle. Secondary forests also result from continuous human uses of forests such as grazing, fuelwood collection and burning. This is particularly true in the drier open forest formations. Logging of forests also creates secondary forests; however, less emphasis will be placed on these types.

Secondary forests vary in age; however, we will concentrate on forests that are <60–80 yr-old because to the casual observer, forests beyond this age are often indistinguishable from primary forests (Budowski 1961, Richards 1955) and are included in the 'undisturbed' or primary forest category of the Food and Agriculture Organization's assessment of tropical forests (Lanly 1982). Other people working in tropical forests have also suggested that vast areas of forests considered to be primary or virgin may be late secondary (e.g. Budowski 1961, 1970, Gómez-Pompa & Vásquez-Yanes 1974, Lanly 1982, Richards 1955, Sanford *et al.* 1985) because charcoal and/or pottery shards and other human artifacts are often found in soil profiles. More recently, Gómez-Pompa *et al.* (1987) have demonstrated that large forest areas in the Yucatan Peninsula in Mexico, long believed to be primary forests, are in fact secondary forests once managed by ancient Mayan people to satisfy their food and fibre needs.

## EXTENT AND RATES OF FORMATION OF SECONDARY FORESTS

An indication of the extent of secondary forests, logged and forest fallow, in the tropics is shown in Figure 1. The numbers are conservative estimates because old secondary forests are included in the 'undisturbed' category, not all pathways involving conversion to and from secondary forests are quantified, and secondary forest fallow includes cultivated land. These problems are difficult to overcome because of constraints imposed by present remote sensing technology (Lanly 1982). Secondary forests occur in both types of forest formations recognized by Lanly (1982): 1. closed forests in which the canopy and understorey cover a high proportion of the ground, and they may be evergreen, semi-deciduous, or deciduous and grow in wet, moist or dry climates, and 2. open forests which are mixed broadleaf forest-grassland formations with a continuous grass layer in which the tree canopies cover more than 10% of the ground. Forest fallows or secondary forests are a mosaic of different age forests, including all complexes of woody vegetation derived from the clearing of closed and open forests by shifting cultivation, and patches of uncleared forest and agriculture plots (Lanly 1982). Badly degraded sites where fallow is very short or where forest regeneration is unlikely are not included in the forest fallow definition.

Secondary forests occupy a significant fraction of the tropical closed forest formations, composing about 31% of the total forest land (Figure 1). Secondary forests in the open forest formations are less extensive, accounting for about 19% of the forest land area. The area of closed secondary forests created by logging was predicted to grow slowly during 1981–85 because their rate of formation from undisturbed forests was only slightly higher than their rate of conversion to shifting cultivation/forest fallow (Lanly 1982). The area of younger secondary forests (forest fallow) of the closed formations was predicted to grow at the fastest rate.

Geographical differences occur in both the extent and rates of formation of secondary forests. Most secondary forests created by logging are located in tropical Aisa (47%) followed by tropical America (32%) and tropical Africa (21%). In contrast, most secondary forest fallow is in tropical America (46%, Lanly 1982) with the remainder about equally divided between tropical Asia and Africa. Furthermore, most of the closed forest lands in tropical America being converted to secondary forests originate as 'undisturbed' forests (58%), whereas in tropical Asia and Africa most of the closed forest land converted to secondary forest fallow originates as logged forests (72–76%). These regional differences in the type of forest land being cleared for agriculture and forest fallow will surely influence their composition, processes and potential uses.

## VALUES OF SECONDARY FORESTS

It is clear from the above that secondary forests are increasing in area throughout the tropics. At a time when most public attention is focused on the loss of tropical forests, it behoves ecologists and foresters to carefully consider the characteristics of secondary forests because efforts to conserve biological diversity in the tropical biome may rest on how these forests are managed. There are several reasons why secondary forests are so important to conservation in the tropics.

Table 1. Values of secondary forests for human use.

| Value | Source |
|---|---|
| Provide fruits, medicinal plants, construction materials and animal browse | Sabhasri 1978 |
| Produce valuable timber species because they are often dominated by few species (e.g. *Aucoumea klaineana* Pierre., *Cordia alliodora* (Ruiz & Pav.) Oken., *Swietenia macrophylla* King) | Richards 1955, Budowski 1965, Rosero 1979 |
| Produce a uniform raw material with respect to wood density and species richness | Ewel 1979 |
| Wood of secondary species tends to be low in resins, waxes etc., which facilitates their use | Ewel 1979 |
| Produce biomass at a fast rate | Ewel 1979 |
| Relatively easy to regenerate naturally | Ewel 1979 |
| May support higher animal production and serve as productive hunting grounds | Ewel 1979, Posey 1982, Lovejoy 1985 |
| Presence of greater number of vertebrates may enhance tourism | Lovejoy 1985 |
| Secondary species often have properties that foresters seek as suitable for plantations | Ewel 1979 |
| Generally more accessible to markets than remaining primary forests, therefore they have a locational advantage as a source of raw material | Wadsworth 1984 |
| Serve as foster ecosystems for valuable late secondary species | Ewel 1979 |
| Serve as a useful template for designing agroecosystems | Ewel 1986 |
| Restore site productivity and reduce pest populations | Ewel 1986 |

First, these forests are products of human activity and are usually located near human settlements. It is known that secondary forest tree species have many ecological characteristics that make them valuable and useful to people (Table 1). Considerable pressure will be removed from primary forests if secondary forests can be managed sustainably to satisfy some of the human needs that led, in the first place, to the conversion of primary forests. In fact, because of their proximity to the loci of human activity, sustainable use of secondary forests could slow down the chronic expansion of human settlements into virgin territories.

Secondly, secondary forests are fast growing ecosystems whose species life cycles coincide with those of human land uses (Table 2). In fact, the rate of net primary productivity of secondary forests exceeds that of primary forests by a factor of 2 (discussed below). Significant areas of primary forests would not be required for human consumption if a fraction of the net primary productivity of secondary forests could be channelled towards useful human products. It has been pointed out that there is a trend of decreasing importance for wood-based products that are insensitive to the characteristics of the raw material, in other words a strategy of whole-tree any-tree use (Chudnoff 1969, Lugo 1987). As new technologies develop in the wood products industry, secondary forests will become even more valuable for meeting the demands for wood-based products in the future. In short, the high productivity of secondary forests is an asset for conservation of primary forests.

Finally, even if the primary productivity of secondary forests was not used directly by humans, secondary forests would still be assets for conservation

Table 2. Ecological characteristics of secondary forests.

| Characteristics | Source |
|---|---|
| Fast growth rates and short life-spans | Budowski 1965 |
| Number of reproductively mature individuals per species is higher than in mature forests | Zapata & Arroyo 1978 |
| Provide conditions suitable for recolonization of mycorrhizae after agriculture | Ewel 1986 |
| Short life cycles which are adapted to the time cycles of human use of the land | Gómez-Pompa & Vásquez-Yanes 1974 |
| Secondary species produce many seeds that are widely dispersed | Budowski 1965, Gómez-Pompa & Vásquez-Yanez 1974, Opler *et al.* 1980 |
| Seeds of secondary species remain viable in the soil for long time periods (up to several years) | Gómez-Pompa & Vásquez-Yanes 1974, Lebrón 1980 |
| Secondary species often germinate and grow on impoverished soils suggesting low nutrient requirements | Gómez-Pompa & Vásquez-Yanes 1974 |

due to their many other biotic characteristics (Table 2). For example, some secondary forests foster, within their understorey, species that will form future and more mature ecosystems. In many instances, secondary forests provide conditions that help improve soil and water quality or which conserve genetic material, nutrients, moisture and/or soil organic matter. All of these functions are of great importance to the conservation of biodiversity in the tropics.

All the functions of secondary forests depend on their ecological characteristics. Proper management of these characteristics will depend on how well they are understood. Yet, scientific understanding of tropical secondary forests is poor at best. We identified only about 30 sources where quantitative studies of tropical secondary forests had been undertaken (Table 3). Data available, however, provide a sound basis for further study and development of research priorities. We group the results into five subjects: 1. species richness, 2. complexity of vegetation, 3. biomass, 4. primary productivity, and 5. nutrient cycling.

## SPECIES RICHNESS

The data assembled show that secondary forests accumulate woody plant species at relatively rapid rates such that within a span of 80 yr or less, the number of species approaches that of mature forests (Table 4). In some of the examples, the recovery of species numbers was much faster than 80 yr, and in others, the secondary forest had more species than the mature forest it replaced.

There are many factors that influence the recovery of species composition in an ecosystem. For example, in recently cut and cleared dry forests, stem coppicing and root sprouting are mechanisms that rapidly restore the number of species on a given site (Murphy & Lugo 1986). The availability of seed sources is another factor that regulates the recovery of numbers of species in forests that regenerate by seed (Uhl & Clark 1983). The influence of seed availability is particularly important for secondary forests growing in large disturbed areas. When seed sources are far from the damaged site, seed vectors determine the rehabilitation of species richness (Uhl 1988). The nature of the disturbance that created the secondary forest is also a regulating factor of the number of species. However, the mechanism of action of this factor is complex because its effect depends on: 1. its intensity, 2. its rate of recurrence (chronic or acute), and 3. its point of interaction with the forest (Lugo 1978, e.g. does it affect the seed pool, mature plants only, all plants as opposed to some, etc.?).

The data available in Table 4 do not allow generalizations on any of these factors because contrasting trends are exhibited. These contrasting trends are most likely due to a number of factors including the intensity and type of the previous disturbance and climate-induced differences in the mechanisms by which plants become established; for example, from root sprouting or coppicing in dry forests versus from seeds in humid forests (Ewel 1977, Murphy & Lugo 1986). The size of the plots in which the species richness data were collected is also a factor preventing generalizations because in most cases the plot sizes were small, $<0.5$ ha.

Because secondary forests are extensive over the tropical landscape large sample areas are needed to assess their full species complement. When the sample area is expanded to the scale of thousands of hectares, as in forest inventories, the number of species encountered rises sharply (e.g. Birdsey & Weaver 1982 in Table 4). The total number of species of trees in secondary forests derived from agriculture (the majority of which were less than 30 yr-old) in Puerto Rico, on an island-wide basis, was 172. The secondary forests derived from abandoned coffee plantations were less species rich than those derived from agriculture (Table 4) because the few species used for coffee shade now dominate the stands (Birdsey & Weaver 1982). This is clearly an example of how past land-use directly influences the species composition of secondary forests for several decades.

Another aspect of the issue of species recovery is the kinds of species that predominate in secondary forests. One could argue that the *number* of species is not as important as the *kinds* of species. One basis for this argument is the value attached by many to rarity. A large number of species in mature forests is due to the presence of rare species. In contrast, secondary forests are usually composed of common species.

Because mature and secondary forests represent opposite states of ecosystems, we argue that numbers of species is more revealing than the kinds of species present. As ecosystems progress through reorganization, aggradation, and transition phases which lead to the steady state phase (*sensu* Bormann & Likens 1981), growth conditions change. Usually the kinds of species also change. Thus, one cannot expect to find early successional species (usually light adapted in their seedling and sapling stages; Bazzaz & Pickett 1980) under closed canopies, nor does one expect shade-adapted species when the canopy is open. Light adaptation and availability often dictate a progression of species

Table 3. Sources of data used in this review.

| Country | Rainfall (mm yr$^{-1}$) | Life zone[1] | Soil | Ages (yr) | Disturbance history | Type of data | Study No. | Source |
|---|---|---|---|---|---|---|---|---|
| Nigeria | 1300 -1600 | T-df | Highly weathered oxisol | 10 replicate plots of 1, 3, 7, 10, and mature | Shifting cultivation | Forest structure, soil nutrients | 1 | Aweto 1981a, b |
| Yangambi, Belgian Congo | ≈2000 | T-mf | – | 2, 5, 8, 17-18 | Shifting cultivation | Biomass and nutrient content | 2 | Bartholomew *et al.* 1953 |
| Thailand | 1150 | S-mf | – | 1, 3, 6, 9, 20+, old secondary | Shifting cultivation | Biomass | 3 | Drew *et al.* 1978 |
| Puerto Rico | 900 | S-df | Entisol | 13, old secondary | Cut only | Forest structure | 4 | Dunevitz 1985 |
| Darien Province, Panama | 2000 | T-mf | Poorly drained alluvium and upland terrace | 2 replicate plots of 2, 4, 6 | One or more shifting cultivation cycles | Biomass and production | 5 | Ewel 1971, 1975 |
| Guatemala | 2000 | S-mf Δ wf | Alluvial soils | 1, 3, 4, 5, 6, 9, 14, mature | Shifting cultivation | Litterfall and decomposition | 6 | Ewel 1976 |
| Sarawak | 4200 | T-wf | Deeply weathered and recent alluvium | 4.5, 4.5, 9.5 | Logged, followed by shifting cultivation | Biomass and forest structure | 7 | Ewel *et al.* 1983 |
| Colombia | 3000 | T-mf | – | 2, 5, 16 and two primary forest sites | Cleared, burned but not cultivated | Biomass, litterfall, and nutrient content | 8 | Fölster & de las Salas 1976, Fölster *et al.* 1976 |
| Ghana | 1650 | T-df | – | ≈40 | Cultivated about 30-50 yr | Biomass, nutrient content, and litterfall | 9 | Greenland & Kowal 1960, Nye 1961 |
| Trinidad | 1900 | T-df | – | 3 sites: 7, 15-16, a very late secondary | Complete clearing and cultivation for 20-30 yr | Forest structure | 10 | Greig-Smith 1952 |
| Nigeria | 1280 | T-df | – | 8 | Cocoa plantation, cultivated for several decades | Forest structure | 11 | Hall & Okali 1979 |
| Puerto Rico | 3000 | S-wf | – | 44 | – | Biomass and production | 12 | Jordan & Farnworth 1982 |
| Mindanao, Philippines | 4200 | T-PM-wf | – | 13 sites: 1, 2.5, 6.5 7 (×2), 19 (×4), 21, 27 (×2), mature | Various disturbances: cleared, burned, cultivated, logged | Forest structure and litterfall | 13 | Kellman 1970 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Kepong, Malaysia | – | – | – | Same plot measured 4 times at 2, 4, 15, 31 | Farmed, tree plantation, cleared and cultivated | Forest structure | 14 | Kochummen & Ng 1977 |
| Puerto Rico | 3500 | S-wf | Ultisol | Approximately 6, 20, 21, 50 | Cultivated | Biomass, litterfall, and nutrient content | 15 | Lugo, unpublished |
| French Guiana | – | T-mf | – | 5 plots of 3.5 | Clear cut for logging | Biomass | 16 | Maury-Lechon 1982 |
| Nigeria | 1830 | T-df | – | 6 | Shifting cultivation | Biomass and nutrient content | 17 | Nye & Greenland 1960 |
| Costa Rica | 4100 | T-wf | 2 plots on sand bank and high plateau | 15 | (presently managed) | Forest structure | 18 | Rosero 1979 |
| Nigeria | 1280 | T-df | – | 5, 14, 17 | Shifting cultivation (2–3 yr cycle) | Forest structure | 19 | Ross 1954 |
| Thailand | 1400 | S-LM-wf Δmf | – | 4, 7, 10, old-growth | Shifting cultivation (1–2 yr cycle) | Biomass | 20 | Sabhasri 1978 |
| San Carlos, Venezuela | 3520 | T-mf | Sandy (80–90% sand) | 3 to 4 replicate plots: 10, 20, 35, 60, 80, mature | Shifting cultivation | Biomass and forest structure | 21 | Saldarriaga *et al.* 1986 |
| India | – | S-mf | Deep, alluvial loam | 40–43 | Cleared | Biomass and nutrient content | 22 | Singh 1975 |
| India | 2200 | S-mf-Δwf | – | 50 | Fuelwood collection | Biomass | 23 | Singh & Ramakrishnan 1982 |
| Guatemala | 2000 | S-mf-Δwf | – | 10 sites: 1–10 | Shifting cultivation | Biomass | 24 | Snedaker 1970 |
| Nigeria | – | T-df | – | 3 sites: 5–8 | Shifting cultivation | Litterfall and decomposition | 25 | Swift *et al.* 1981 |
| India | 2200 | S-mf-Δwf | Oxisol | 3 replicates of 1, 10, 15, 20 | Shifting cultivation (5–30 yr fallow cycles) | Biomass, litterfall, decomposition, nutrient content, and soil | 26 | Ramakrishnan & Toky 1981 Toky & Ramakrishnan 1983a, 1983b, 1984, |
| San Carlos, Venezuela | 3520 | T-mf | – | 1–5 | Shifting cultivation | Biomass and litterfall | 27 | Uhl 1987 |
| Mexico | 3640 | S-wf | Oxisol and alfisol | 7 | Cut and cleared, cultivated 1 yr | Biomass and nutrient content | 28 | Williams-Linera 1983 |
| Venezuela | 760 | T-PM-df | – | 40 | ? | Forest structure | 29 | Zapata & Arroyo 1978 |

[1] T = tropical, S = subtropical, df = dry forest, mf = moist forest, wf = wet forest, PM = premontane, LM = lower montane, Δ = transition.

Table 4. Species richness of woody plants in secondary forests, arranged by life zone.

| Age (yr) | Disturbance[1] | Area (ha) | Number of species: Trees | Shrubs | All | Source number[2] |
|---|---|---|---|---|---|---|
| | | *T-wet forest* | | | | |
| 10 | Shifting cultivation plots | 0.36 | – | – | 23 | 21 |
| 20 | | 0.36 | – | – | 42 | |
| 35 | | 0.39 | – | – | 44 | |
| 60 | | 0.27 | – | – | 49 | |
| 80 | | 0.30 | – | – | 62 | |
| Mature | – | 0.36 | – | – | 67 | |
| | | *T-premontane wet forest* | | | | |
| 1 | CB, c-1 | 0.045 | – | – | 48 | 13[3] |
| 2.5 | C | 0.045 | – | – | 45 | |
| 6.5 | CB, c-1 | 0.045 | – | – | 66 | |
| 7 | CB | 0.045 | – | – | 77 | |
| 7 | CB, c-14 | 0.045 | – | – | 46 | |
| 19 | C, c-1 | 0.045 | – | – | 55 | |
| 19 | CB | 0.045 | – | – | 61 | |
| 19 | CB | 0.052 | – | – | 61 | |
| 19 | C | 0.052 | – | – | 50 | |
| 21 | CB, c-2 | 0.052 | – | – | 93 | |
| 27 | CB | 0.045 | – | – | 78 | |
| 27 | CB | 0.052 | – | – | 81 | |
| Mature | – | 0.045 | – | – | 85 | |
| | | *T-dry forest* | | | | |
| 7 | C, c-30 | 0.09 | – | – | 53 | 10 |
| 15–16 | C, c-22 | 0.09 | – | – | 45 | |
| Late secondary | – | 0.09 | – | – | 36 | |
| 1 | Shifting cultivation plots | 0.09 | 2 | – | 39 | 1[3] |
| 3 | | 0.09 | 7 | – | 43 | |
| 7 | | 0.09 | 15 | – | 57 | |
| 10 | | 0.09 | 19 | – | 54 | |
| Late secondary | | 0.09 | 25 | – | 61 | |
| 5 | Shifting cultivation plots (2–3 yr cycle) | 0.19 | – | – | 60 | 19 |
| 14 | | 0.19 | – | – | 63 | |
| 17 | | 0.37 | – | – | 67 | |
| 8 | C, c ~decades | 3.125 | – | – | 308[3] | 11 |
| | | 0.50 | – | – | 70 | |
| 40 | ? | 2.0 | 22 | – | 93 | 29 |
| | | *S-wet forest* | | | | |
| 6 | Cultivation | 0.20 | 17 | – | 35 | 15 |
| 20 | | 0.20 | 24 | – | 46 | |
| 21 | | 0.20 | 19 | – | 40 | |
| 50 | | 0.20 | 37 | – | 45 | |
| | | *S-moist/wet forest* | | | | |
| Secondary[4] | Agriculture | 59200 | 172 | – | – | Birdsey & Weaver 1982 |
| Secondary[5] | Abandoned coffee | 38200 | 81 | – | – | |
| Secondary[6] | Agriculture/abandoned coffee | 15739 | 69 | – | – | Birdsey & Jiménez 1985 |

Table 4 - *continued*

| Age (yr) | Disturbance[1] | Area (ha) | Number of species: Trees | Shrubs | All | Source number[2] |
|---|---|---|---|---|---|---|
| | | *S-dry forest* | | | | |
| 13 | C | From species | – | – | 80 | 4[3] |
| Late secondary | | area curve | – | – | 49 | |
| | | *Life zone unknown* | | | | |
| 2 | C, c∼decades, | 0.09 | – | – | 29 | 14 |
| 4 | 12 yr as | 0.09 | – | – | 26 | |
| 15 | plantation, | 0.09 | – | – | 25 | |
| 31 | and C, c∼3 | 0.09 | – | – | 51 | |
| Young secondary | Agriculture | 3570 | 39 | – | – | Birdsey *et al.* |
| Secondary | Agriculture | 3706 | 36 | – | – | 1986 |

[1] Disturbance history: C = cleared, B = burned, c = crops, followed by number of years crops were grown.
[2] See Table 3 for more details.
[3] Includes herbaceous species.
[4] 71% of area is <30 yr-old, 25% is >30 yr-old, and 4% is of mixed ages.
[5] 44% of area is < 30 yr-old, 47% is >30 yr-old, and 9% is of mixed ages.
[6] Mixed ages.

as conditions change. The same may be true of other environmental factors such as moisture or nutritional gradients. On the other hand, if the number of species is large during the reorganization and aggradation phases of ecosystem development (which correspond to early secondary forests in the tropics) this indicates that the opportunities for species establishment are high. If so, the secondary forest is behaving as a species refugia. The higher the initial number of species that it can sustain, the greater its role as a foster ecosystem because more species combinations (plants and animals, symbiotic relations, etc.) can occur.

The fostering of the mature forest species by those in the secondary forest can be illustrated by two examples. The first one is the maturation of secondary forests in Puerto Rico (Birdsey & Weaver 1982, 1987). In examining the species composition of these forests, they found that the dominant canopy species reflected previous land uses. Ten species accounted for almost 50% of the basal area of the Puerto Rican secondary forests, derived from both agriculture and abandoned coffee, and nine of these ten were introduced fruit trees, coffee shade trees, and ornamental or shade trees (Birdsey & Weaver 1982). The other 50% of the basal area was composed of 179 tree species (total tree species = 189, 172 of which were on abandoned agriculture land; of the 81 species found on abandoned coffee lands 64 species overlapped with those on abandoned agriculture). Thus the understorey of these 'human made' secondary forests was rich in native species that were typical of late secondary and mature forests (Wadsworth & Birdsey 1985). Coffee shade and ornamental tree species did not do well in these understoreys. After 5 yr the trend towards species enrichment by native species found in the first inventory had accelerated.

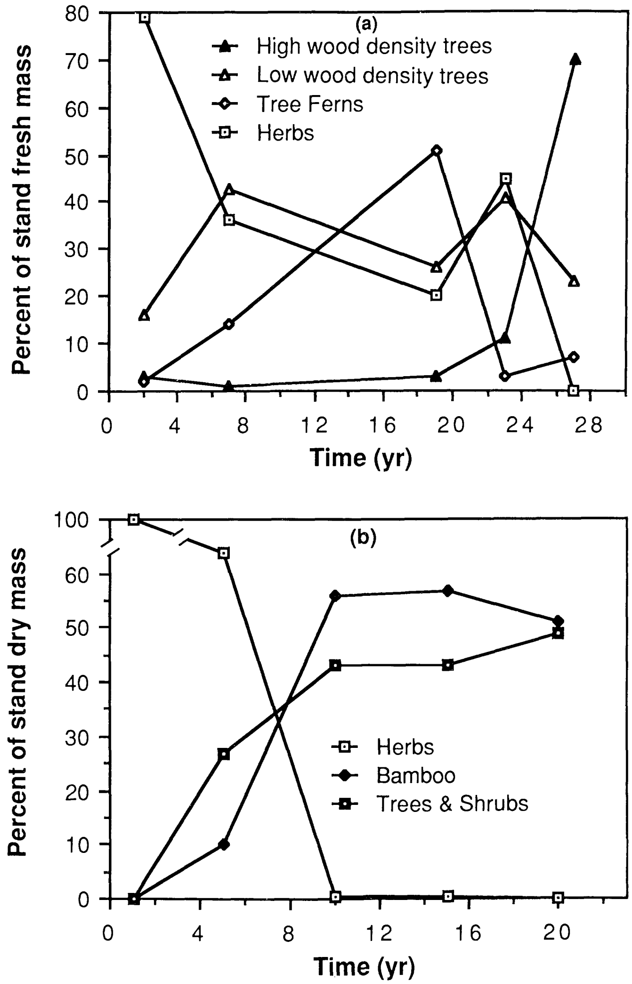


Figure 2. Changes over time in relative mass of life forms of secondary forests in (a) tropical premontane wet forest life zone in the Philippines (data from Kellman 1970) and (b) subtropical moist forest life zone in India (data from Toky & Ramakrishnan 1983a).

A second example is illustrated in Figure 2 which summarizes the pattern of changes in plant life forms of secondary forests in two life zones. Here, life forms replace each other as the system develops. The early successional species develop high leaf area index, provide complete ground cover, accumulate soil organic matter, and make conditions more favourable for further advance in the species that succeed them in succession (Figure 2).

In short, one cannot judge the 'value' of secondary forests only by how common or useful their species are during their early stages of growth. Instead, secondary forests need to be assessed by the potential they offer in terms of facilitating the development of the forest into advanced stages of succession where species richness, the number of rare species, and usefulness to people could be greatly enhanced.

## VEGETATION STRUCTURE OF SECONDARY FORESTS

The vegetation structure of secondary tropical forests is simple in comparison with their mature forest counterparts (Tables 5-6). The characteristics that typify the secondary forests are: 1. high total stem density but low density of trees >10 cm dbh, 2. low basal area, 3. short trees with small diameters, 4. low woody volume (except the managed secondary forests), and 5. high leaf area indices. These trends in the structure of secondary forests apply regardless of the size of the study sites (compare trends in the island-wide inventories with those of smaller research sites in Table 5).

The structural characteristics of secondary forests change with age, and the rate of change is mediated by climate and soil type (Table 5). For example, total stem density decreases, tree density (dbh >10 cm) and individual tree diameter increases, and the stand increases in height, basal area and volume. The leaf area index may reach very high values early in the development of the forest and later decrease to a steady state value.

As secondary forests age, the stand-weighted specific gravity of the forest increases (Saldarriaga *et al.* 1986, Weaver 1986). Therefore, extreme care is needed in arriving at conclusions about the structure and function of secondary forests based on volume or basal area alone. The process of vegetation ageing involves rapid structural change so that indices such as basal area and volume may be similar to those of mature forests decades, or even centuries, before maturity. The differences that accrue later in the development of the forest involve changes in the quality of structure, e.g. the density and chemistry of wood. Many of these qualitative changes are accompanied by the changes in species composition.

## ACCUMULATION OF ORGANIC MATTER IN SECONDARY FORESTS

Live biomass of forests, as a measure, integrates volume and wood density information. The data available for secondary forests (Figure 3) have three salient features: 1. the first 15 yr or so of forest development are characterized by rapid biomass accumulation (up to 100 t $ha^{-1}$) regardless of climatic condition. 2. After 15 yr, forest stands diverge in the amount of biomass accumulated. In mature forest stands the divergence in biomass is dependent on water availability (Brown & Lugo 1982) but the relation is not as clear for secondary forests. History of disturbance is an important factor that may explain the scatter of these data. For example, Kellman (1970) found that the fresh mass of secondary forests of various ages on slightly disturbed sites was consistently higher than that for forests on more severely disturbed sites. 3. Few of the stands accumulated more than 200 t $ha^{-1}$ by age 80 yr. This last observation implies a stagnation in the rate of biomass accumulation which is discussed further below.

Table 5. Structural characteristics of secondary forests arranged by life zone.

| Age (yr) | Minimum dbh measured (cm) | Basal area ($m^2 ha^{-1}$) | Stem density (No. $ha^{-1}$) | Canopy height (m) | dbh (cm) | LAI | Source[1] |
|---|---|---|---|---|---|---|---|
| | | | *T-wet forest* | | | | |
| 4.5 (poor soil) | all stems | 4.3 | 4060 | 6 | – | – | 7 |
| 4.5 (rich soil) | all stems | 16.3 | 3867 | 12.2 | – | – | |
| 9.5 | all stems | 12.7 | 2200 | 11.5 | – | – | |
| 15 | – | 26.9–37.1 | 400–610 | – | 20–25 | – | 18 |
| | | | *T-moist forest* | | | | |
| 10 | 10 | 12.8 | 342 | 10 | – | 5.8 | 21 |
| 20 | 10 | 16.9 | 461 | – | – | 6.9 | |
| 35 | 10 | 18.6 | 495 | 18–19 | – | 6.6 | |
| 60 | 10 | 24.5 | 441 | – | – | 5.6 | |
| 80 | 10 | 24.0 | 604 | – | – | 6.4 | |
| Mature | 10 | 34.8 | 570 | 25–35 | – | 7.5 | |
| 2 | – | – | – | 7.2 | 6 (max) | 7.5 | 5 |
| 2 | – | – | – | 8 | 12 (max) | 6.9 | |
| 4 | – | – | – | 10 | 13.5 (max) | 11.6 | |
| 6 | – | – | – | 12 | 17.5 (max) | 16.5 | |
| | | | *T-dry forest* | | | | |
| 8 | 3.2 | 11.8 | 2038 | 25 (max) | – | – | 11 |
| 3 | 1.0 | – | 512 | 2.5 | 1.8 | – | 1 |
| 7 | 1.0 | – | 2270 | 4.7 | 4.6 | – | |
| 10 | 1.0 | – | 2670 | 5.8 | 7.2 | – | |
| Late secondary | 1.0 | – | 2260 | 10.4 | 20.0 | – | |
| | | | *S-wet forest* | | | | |
| 6 | 10 | 7.2 | 1334 | 10 (max) | – | – | 15 |
| 20 | 10 | 28.5 | 1234 | 25 (max) | – | – | |
| 21 | 10 | 27.8 | 2436 | 19 (max) | – | – | |
| 50 | 10 | 33.8 | 1593 | 24 (max) | – | – | |
| | | | *S-moist/wet forest* | | | | |
| Secondary[2] (from agriculture | 2.5 | 13.8 | 2752 | – | – | – | Birdsey & Weaver 1982 |
| Secondary[2] (from abandoned coffee) | 2.5 | 14.0 | 1728 | – | – | – | |
| Secondary[2] (from agriculture) | 2.5 | 13.5 | 1672 | 12.0 | – | – | Birdsey & Jiménez 1985 |
| Secondary[2] (from abandoned coffee) | 2.5 | 17.2 | 2383 | 15.0 | – | – | |
| | | | *LZ-unknown* | | | | |
| 15 | 2.4 | 6.3 | 274 | 6 (max) | 8.1 (max) | – | 14 |
| 31 | 2.4 | 12.9 | 876 | – | – | – | |
| Young secondary | 2.5 | 16.3 | 2578 | 13.7 | – | – | Birdsey *et al.* 1986 |
| Secondary | 2.5 | 16.9 | 1506 | 20.0 | – | – | |

[1] See Table 3 for more information. [2] See Table 4 for more details on these entries.

Table 6. Forest structure and growth (all trees to a minimum dbh of 10 cm) of some secondary forests.

| Forest disturbance | Commercial volume ($m^3$ $ha^{-1}$) | Volume increment ($m^3$ $ha^{-1}$ $yr^{-1}$) | Estimated wood biomass production[1] (t $ha^{-1}$ $yr^{-1}$) | Time period[2] |
|---|---|---|---|---|
| | *Tropical very dry forest*[3] | | | |
| Fire, grazed and logged | 31.3 | 0.58 | 0.64 | 15.2 |
| | 25.0 | 0.31 | 0.34 | 15.2 |
| Undisturbed (average of 2 stands) | 131.0 | 3.36 | 3.71 | 4.0 |
| | *Tropical dry forest*[3] | | | |
| Fire, grazed | 103.2 | 2.07 | 2.29 | 9.8 |
| Fire, grazed and logged | 111.8 | 1.75 | 1.93 | 8.1 |
| | 137.3 | 1.64 | 1.81 | 6.2 |
| Undisturbed (average of 6 stands) | 208.0 | 4.40 | 4.86 | 17.0 |
| | *Tropical montane moist forest*[3] | | | |
| Logged | 120.3 | 4.20 | 4.64 | 23.9 |
| Undisturbed (average of 3 stands) | 368.0 | 4.15 | 4.59 | 14–24 |
| | *Tropical wet forest*[4] | | | |
| Managed forests (with 8–9 native commercial species), 15 yr-old: | | | | |
| Sand bank near river | 507 | 33.8[5] | 29.7 | – |
| Plateau | 410 | 27.5[5] | 24.2 | – |

[1] The factors for converting commercial volume to wood biomass (specific gravity × [(total wood biomass/commercial biomass]) = 1.1 for dry and moist forests and 0.9 for wet forests (Brown *et al.* in press).
[2] Period of time (yr) during which volume increment was measured.
[3] From Veillon (1985) for plots in Venezuela that had never been cleared.
[4] From source 18 in Table 3.
[5] Volume increment calculated as volume divided by age of stand (= periodic annual increment).

The distribution of biomass provides additional insight into the organization of secondary forests. For example, as with temperate forests, the quantity of dead woody mass tends to increase and its relative contribution to total mass may decline with age (Table 7). Bormann & Likens (1981) used the quantity

Table 7. Quantity of dead woody debris in secondary forests in the tropical moist forest life zone.

| Forest age (yr) | Mass of woody debris (t $ha^{-1}$) | Percentage of live wood | Source number (see Table 3) |
|---|---|---|---|
| 10 | 17.9 | 35.0 | 21 |
| 20 | 1.1 | 1.6 | 21 |
| 35 | 6.1 | 5.4 | 21 |
| 60 | 23.1 | 16.6 | 21 |
| 80 | 16.5 | 12.1 | 21 |
| Mature | 22.7 | 10.1 | 21 |
| 5 | 2.5 | 3.5 | 2 |
| 17.5 | 17.3 | 15.1 | 9 |
| 40 | 72.0 | 41.5 | 9 |

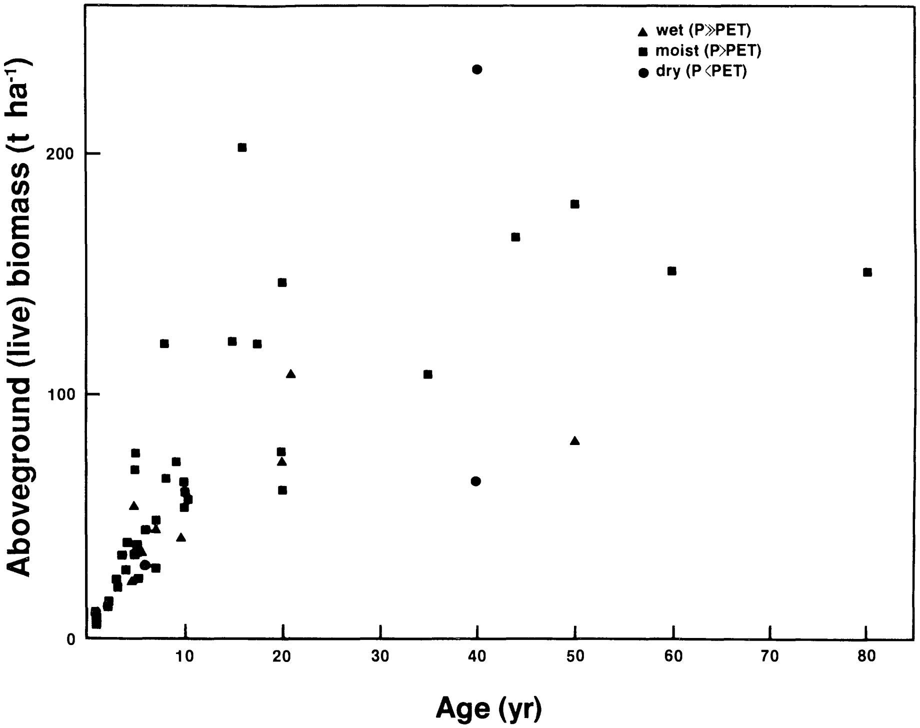


Figure 3. Above ground biomass (excluding litter) of different aged secondary forests. Data are from the following sources keyed to Table 3: 2, 3, 5, 7–9, 12, 15–17, 20–24, 26–28.

of woody debris to delimit the stages of development of temperate forests. They noted that initially dead wood increases as a result of disturbance (e.g. after cutting) and then declines for about two decades due to decomposition. Thereafter dead wood increased as the stands aged. Such a pattern may occur in tropical forests not subject to frequent disturbance because absence of disturbance would allow forests to age and produce a steady increase of dead wood on the forest floor. However, if disturbances are frequent, the pattern may be obscured by continuous production of dead wood. In the tropics the decomposition of wood of many species is also fast (unpublished data from authors) and thus the initial stage may occur in less than 20 yr.

Secondary forests develop maximum leaf biomass early in their development and maintain these values through to maturation (Figure 4). Root biomass accumulates at a somewhat slower rate than leaves, and continues to increase slowly with age. However, biomass of fine roots (<2 mm diameter) may reach values similar to mature forests at a young age (c. 5 yr, for example; Berish & Ewel 1988). In contrast, the relative amount of woody biomass increases rapidly during the first 15–20 yr, followed by a steady but slower rate until maturity. The pattern of biomass allocation has management implications because if stem biomass is the objective of management, not all secondary forests will maximize stem productivity early in their development. Slow initial

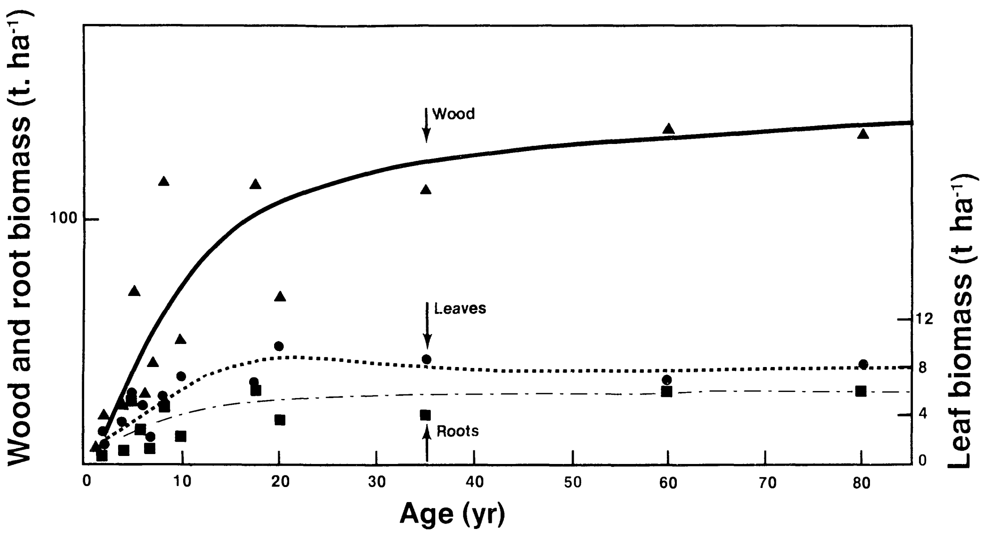


Figure 4. Biomass of leaves, roots and wood (twigs, branches and stems) of different aged secondary forests in tropical moist and wet forest life zones. Lines are drawn by eye to show general trends. Data are from sources, 2, 5, 21 and 28 in Table 3.

stemwood productivity may be discouraging, but in many cases, it is followed by explosive growth once the leaf and root components are fully developed. Patterns such as these explain why short-term research observations of managed systems are often misleading.

The presence of secondary forest vegetation restores soil organic matter pools (e.g. Aweto 1981a, Brown *et al.* 1984, Lugo *et al.* 1986, Ramakrishnan & Toky 1981) because it provides organic matter inputs in the form of above ground and below ground litter. A comparison of soil organic matter content under a chronosequence of secondary forests in three contrasting life zones indicated that the time to reach levels similar to nearby mature forests was approximately the same (about 40–50 yr) regardless of the intensity of the previous agricultural cropping practice and the initial organic matter content (Figure 5). We attribute this to the recovery of organic inputs in the form of litterfall (Figure 6) and high root biomass production (Berish & Ewel 1988, Cuevas, Brown & Lugo, unpublished data) in secondary forests (see next section).

Weaver *et al.* (1987) in their study of soil organic matter under many different aged secondary forests in two contrasting life zones (subtropical moist and wet) concluded that previous agricultural practice influenced the amount of soil organic matter under secondary forests. For example, soils of secondary forests that were preceded by coffee had less soil organic matter than soils of secondary forests preceded by pastures. The data in Figure 5 show that pasture sites in the wet life zone contained as much or more organic matter than many of the secondary forests. Furthermore, soils under pastures in many life zones have also been shown to contain as much or more soil organic matter as the

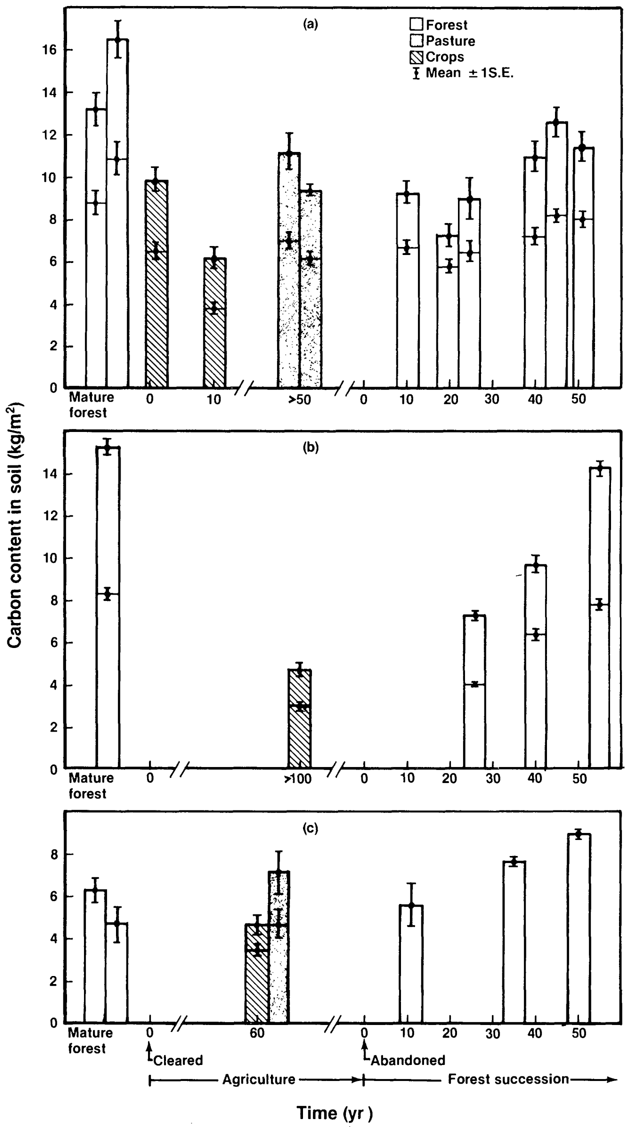


Figure 5. Soil organic carbon contents of sites arranged in chronosequences of forest conversion to agriculture, followed by abandonment and subsequent forest succession. All secondary forest sites were preceded by cropping practices. (a) Wet forest life zone in Puerto Rico, (b) moist forest life zone in St John, Virgin Islands, and (c) dry forest life zone in Puerto Rico. The total height of the bar in (a) and (b) is to a sampling depth of 50 cm and the shorter bar is to 25 cm depth; the total height of the bar in (c) is to a sampling depth of 25 cm (unpublished data from authors).

mature forests that preceded them (Brown *et al.* 1984, Lugo *et al.* 1986, S. Brown, unpublished data).

The above results underscore the importance of knowing the previous land-use history of secondary forests for understanding the processes associated with soil organic matter. To understand further the soil organic matter processes under secondary forests it is also important to have information on soil bulk

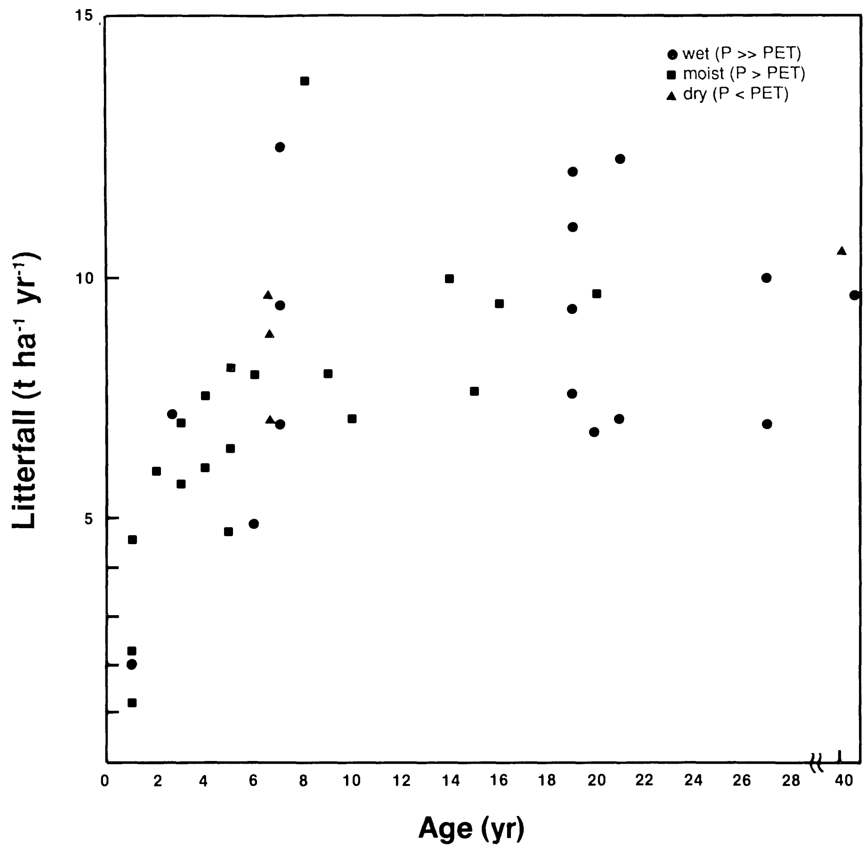


Figure 6. Rates of litterfall of different age secondary forests. Data are from sources 2, 6, 8, 9, 13, 15 and 25–27 in Table 3.

density (it is not enough to compare percent organic matter because bulk density tends to change too) and soil texture (texture, particularly sand and clay which influence soil organic matter; Lugo *et al.* 1986, Sánchez 1976). Without such complete data sets on these soil parameters, misconceptions about soil organic matter dynamics under secondary forests will continue to arise.

## NET PRIMARY PRODUCTIVITY OF SECONDARY FORESTS

We have divided the net primary productivity of secondary forests into two components, wood and leaves; data on root production are lacking. Because woody biomass accumulates rapidly in these forests, particularly in the first 20 yr (Figure 4), it is imperative that rate measurements be based on as short a time interval as possible. Rates of wood production based on short-term measurements (1–2 yr) are variable and range between 2–11 t $ha^{-1}$ $yr^{-1}$ (Ewel 1971, Toky & Ramakrishnan 1983a, A. E. Lugo, unpublished data). These rates are higher in general than those for mature tropical forests (1–8 t $ha^{-1}$

$yr^{-1}$; Brown & Lugo 1982 and Table 6). For older secondary forests (>40 yr), data on rates of wood production are few and range between <1–4.5 t $ha^{-1}$ $yr^{-1}$ (Table 6, Jordan & Farnworth 1982, Singh 1975, A. E. Lugo, unpublished data). The climate in which the forest grows appears to explain partly some of the variability in these data (Table 6). High production of wood biomass appears to be possible if the secondary forest is intensively managed (Table 6). Weaver 1986) reported mean annual rates of woody biomass accumulation, for forests in tropical America, to range from about 1–11 t $ha^{-1}$ $yr^{-1}$ for forests <10 yr-old compared to <2 t $ha^{-1}$ $yr^{-1}$ for mature forests.

Because leaf biomass of secondary forests quickly reaches a steady state (Figure 4), we assume that litterfall data can be used as an index of net production of leaves. Available data on the production of litter in secondary forests show three trends (Figure 6): 1. continued increase in rate for about 12–15 yr, 2. a limit at about 12–13 t $ha^{-1}$ $yr^{-1}$, and 3. no particular trend with climatic conditions. However, data for mature forests did show a significant relation with climate (Brown & Lugo 1982, Vitousek 1984). It is possible that the few available data, particularly in dry forest life zones, do not allow any relation with climate to be exhibited.

The trends just described have important implications to the dynamics of secondary forests. For example, litter production in young secondary forests (<20 yr) is a higher fraction of total net above ground primary production than stemwood biomass production. Furthermore, leaf decomposition of secondary species is fast (Ewel 1976, Swift *et al.* 1981, Toky & Ramakrisnan 1984). Therefore, more organic matter is turning over than is stored either in live (wood) or dead (litter) compartments. This turnover of dead parts is important to the nutrient demands on, and return to, the soil. The rapid increase in litter production during the first 15 yr of the stand (increasing from a low of 1 to as much as 12 t $ha^{-1}$ $yr^{-1}$; Figure 6) demonstrates the magnitude of structural development and destruction that occurs during the first two decades of a secondary forest. At an average litterfall rate of 8 t $ha^{-1}$ $yr^{-1}$ over 20 yr (Figure 6), the forest would produce and discard 160 t $ha^{-1}$ of mass while storing above ground an additional 140 t $ha^{-1}$ (Figure 3). This averages to a total net above ground production of about 15 t $ha^{-1}$ $yr^{-1}$, a very high rate.

## NUTRIENT CYCLING IN SECONDARY FORESTS

Secondary forests are nutrient sinks (Vitousek 1984, Vitousek & Reiners 1975, Table 8 and Figure 7). They accumulate nutrients rapidly with time (Table 8), although the proportion of nutrients accumulated in vegetation, litter and soil varies with element (Figure 7). In spite of the differences in soil types and depth among the sites presented in Figure 7, general trends are apparent for N and P. For example, the amount of N and total P in the soil exceeds that in vegetation plus litter in all sites, regardless of age. In contrast, the amount of available P in soil is less than that in vegetation and litter. No general pattern of distribution is exhibited for K, Ca and Mg.

The nutrient sink function of secondary forest vegetation is magnified in the first decades of development relative to its function as a carbon sink because young trees tend to accumulate nutrients in contrast to old trees which tend to re-use them (Bowen & Nambiar 1984). That is, a higher fraction of the total nutrient storage at maturity is taken up early in the development of a forest than the corresponding value for organic matter storage. As forests age, nutrient concentrations in their biomass are diluted by the increase in non-functional biomass with low nutrient concentration.

This characteristic of secondary forests has implications for the management of nutrient reservoirs in forest stands. Unless the objective is to release nutrients, cutting of early secondary vegetation is an inefficient way of using the nutrient capital in the stand because at these early stages the nutrients have not been utilized fully by trees. With time, nutrient-use efficiency will increase as more organic mass is accumulated with diminishing nutrient uptake and greater nutrient re-utilization.

Secondary forests accumulate small amounts of nutrients in their litter compartment (Figure 7), but return large amounts in litterfall (Figure 8). This means that nutrient turnover in litter is extremely high, placing a premium on nutrient recycling or, alternatively, nutrient loss. There are few data on nutrient loss from secondary forests, but if these losses are small as suggested by Vitousek & Reiners (1975), then nutrient uptake from decomposing litter by the rapidly growing vegetation must be high, at least during the first stages of ecosystem development. Later, with the accumulation of dead organic matter

Table 8. Total quantity of nutrients stored in vegetation, litter and soils of some tropical secondary forests growing in moist and wet life zones. The relative proportions of nutrients in vegetation, litter and soil for these sites are shown in Figure 7.

| Site age (yr) | Soil depth (cm) | N | Total P | K | Ca | Mg | Source[1] |
|---|---|---|---|---|---|---|---|
| | | $(kg\ ha^{-1})$ | | | | | |
| 1 | 40 | 1011 | 20[2] | 1031 | 1372 | 1303 | 26 |
| 5 | 40 | 11248 | 30[2] | 761 | 885 | 1154 | |
| 10 | 40 | 12458 | 51[2] | 805 | 1211 | 819 | |
| 15 | 40 | 10913 | 61[2] | 2163 | 1378 | 1356 | |
| 20 | 40 | 11011 | 91[2] | 2587 | 1534 | 1448 | |
| 2 | 50 | 5026 | 212 | 236 | 171 | 83 | 8 |
| 5 | 50 | 8184 | 368 | 556 | 644 | 206 | |
| 16 | 50 | 7685 | 289 | 615 | 743 | 246 | |
| 8 | 15 | 1006 | 61 | 1578 | – | – | 2 |
| 18 | 15 | 1220 | 181 | 994 | – | – | |
| 6 | 100 | 5404 | 977 | 25155 | – | – | 15 |
| 20 | 100 | 8892 | 2812 | 19133 | – | – | |
| 21 | 100 | 8583 | 1224 | 27425 | – | – | |
| 50 | 100 | 9348 | 2258 | 21435 | – | – | |

[1] Refer to Table 3 for more details. [2] Available P.

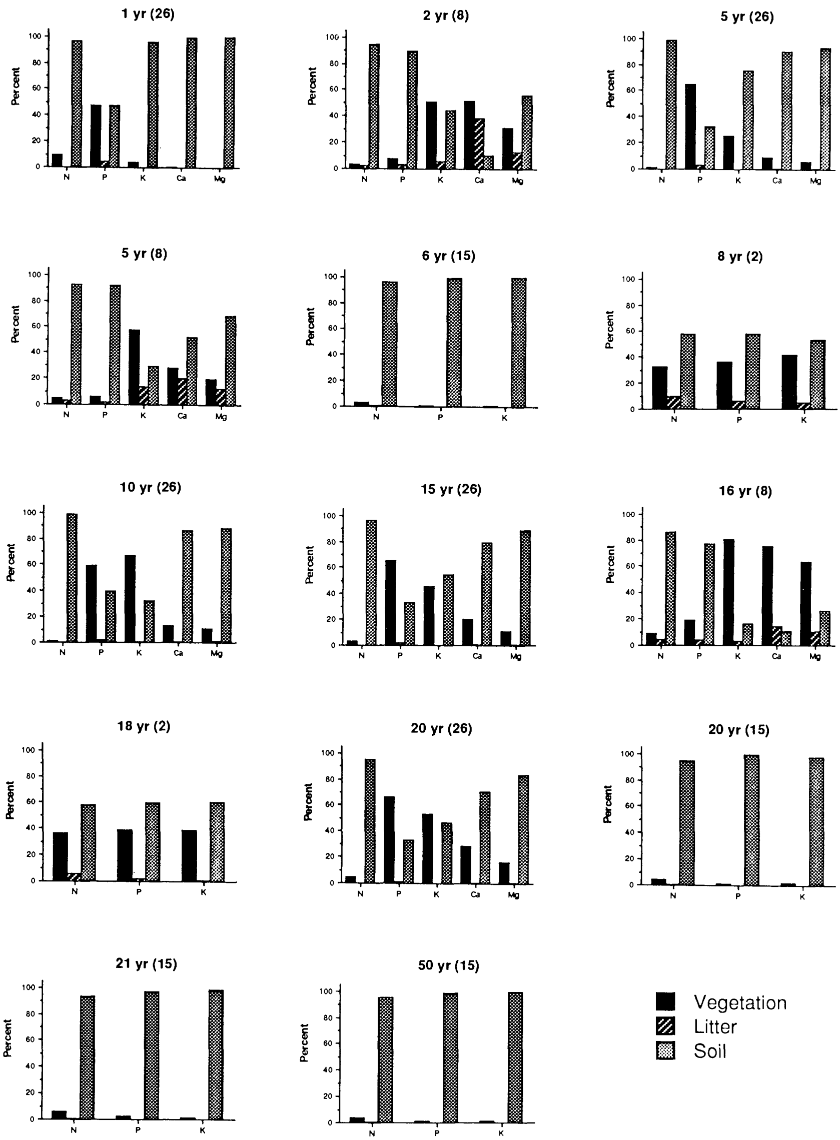


Figure 7. Percent distribution of nutrient contents in vegetation, litter and soil compartments of secondary forests growing in moist and wet environments. The number in parentheses following the age of the forests represent the data sources keyed to Table 3. Refer to Table 8 for absolute quantities of nutrients in these sites.

and litter, and increased vegetation structure, the turnover of nutrients may be slower.

The ratio of litterfall to the amount of nutrients in litterfall was proposed by Vitousek (1984) as a measure of within-stand nutrient cycling efficiency in forests. This ratio, referred to as efficiency of within-stand nutrient use (NUE), is useful for understanding one aspect of the nutrient dynamics of forest ecosystems. Nutrient-use efficiencies of N, P and Ca for secondary forests are

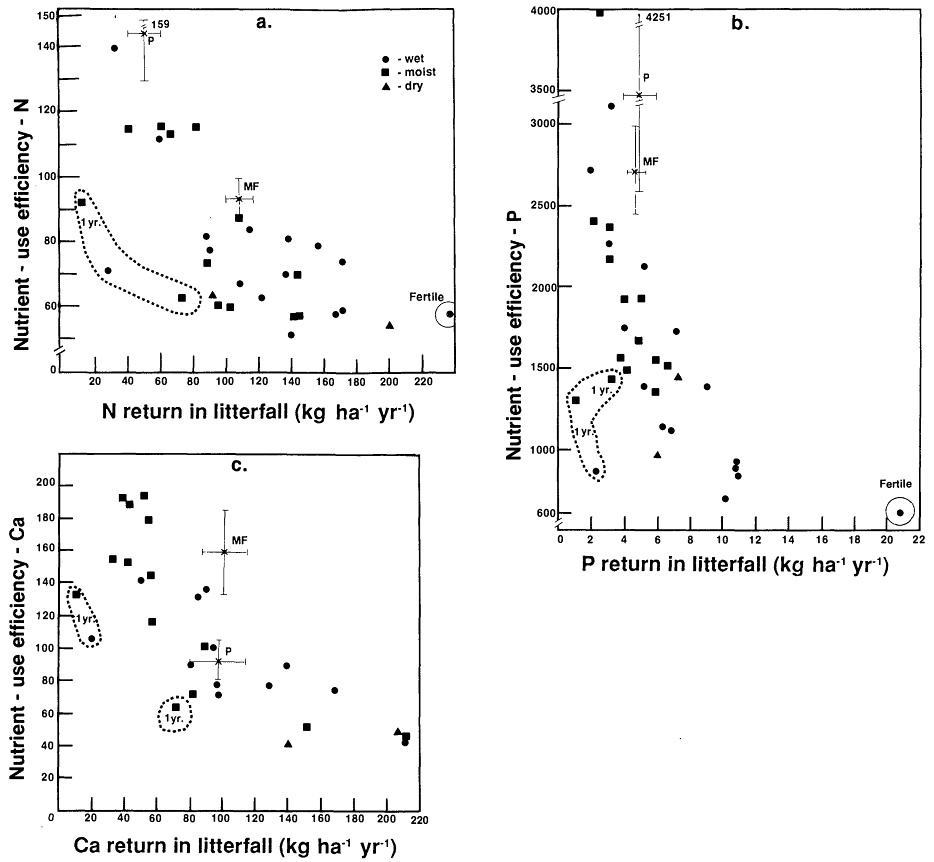


Figure 8. Within-stand nutrient-use efficiency ratios versus nutrient return in litterfall for secondary forests; (a) nitrogen, (b) phosphorus and (c) calcium. Data are from sources 6, 8, 9, 13, 15 and 25–26 in Table 3. Points MF and P are the mean ±1 SE of the nutrient-use efficiency ratio and nutrient return for mature forests and plantations, respectively (data from Vitousek 1984). Dotted lines encompass 1-yr-old stands.

shown in Figure 8. Wet forests tend to have higher NUE for all elements than moist and dry forests. The amount of organic matter produced as litter per unit of nutrient return varied widely, more than four-fold for P and Ca and about three-fold for N. The rate of P return was uniformly low in most secondary forests suggesting that they all retain P in the vegetation.

Although 1-yr-old stands returned few nutrients in litterfall (because of low litterfall, cf. Figure 6), they were as efficient as older secondary stands in the use of N and Ca but less efficient in their use of P. This trend suggests that the pioneer vegetation is less conservative with P and as conservative with N and Ca as more mature vegetation.

Vitousek (1984) presented data on nutrient return in litterfall for about 40 mature stands which we compared with our data on secondary stands (Figure 8). Secondary forests are generally less efficient than mature stands in their return of nutrients to the forest floor, regardless of age, soil type (fertile to infertile), and disturbance history. This trend is particularly noticeable with P; all but three sites are less efficient in their use of P and most secondary forest sites return more P in litterfall than mature forests. This result was anticipated from our discussion on the predominance of nutrient uptake by young trees in secondary forests as opposed to a predominance of nutrient re-use by old trees. The results suggest that secondary forests are accelerating the return of nutrients, particularly P, to the forest floor. If the original uptake by pioneer vegetation was from mineral soil, the forests are in essence pumping nutrients from the mineral to the organic fraction of soils and doing so faster than mature forests. The fact that all secondary forest sites originated from agriculture (and mostly from abandoned shifting cultivation plots), where we expect the top few centimetres of soil to be nutrient poor and quantity of surface litter to be very low, provides support for this argument. However, it is possible that rates of mineralization are high in secondary forests because of the high turnover of litter and the large amount of organic matter that is added to the soil of these forests by litterfall and probably by root mortality. Alternatively, one could argue that secondary forests may have higher soil nutrient availability than mature forests.

Secondary forest stands appeared to respond more to P than to N and Ca because the rate of change of NUE with P return in litterfall is steep. However, the NUE's are smaller than those reported for mature stands. A comparison of secondary forests with plantation stands in Vitousek's (1984) data set shows that the former are less efficient with respect to N and P and similar with respect to Ca than plantations.

In summary, the nutrient cycling strategy of secondary forests appears to be one of rapid nutrient accumulation in vegetation, fast return by litterfall, probably accompanied by rapid turnover and uptake by roots. Because so much organic matter is being produced and decomposed during the first 20 yr of forest development and storages are increasing so fast in the vegetation, we hypothesize that the impact of secondary forests on soil organic matter and fertility is most intense during this period and decreases in rate over time. Later stages of development may have a greater accumulative effect on soil processes, but this is due to the longer time of activity rather than the intensity of processes.

For management purposes secondary forests present a unique challenge. On the one hand they are extremely productive and it is tempting to channel this productivity to immediately useful products. Such a strategy will have a high cost, particularly in the use-efficiency of the nutrient capital of the soil. Alternatively, many of the ecological functions of secondary forests (e.g. maintenance of water and soil quality) bear fruit after 20 yr of development when biological processes associated with rapid change and high net primary productivity begin to slow down. Managing for these values is at the expense of high short-term gains. Managing for the full suite of values of secondary forests, e.g. after the system has had several turnovers of organic matter and floristic composition, requires 50–80 yr and at this time these systems are at the threshold of reaching a steady state when net ecosystem productivity rapidly approaches zero.

## SECONDARY FORESTS AND PEOPLE

It is axiomatic that forests, and secondary forests in particular, are essential to people in the tropics. Some of the uses and values of secondary forests are summarized in Table 1. One of the best documentations of how people interact with secondary forests are the accounts of Gómez-Pompa (1987), Gómez-Pompa & Kaus (1988), and Gómez-Pompa *et al.* (1987). This series of articles reconstructs Mayan dependency on secondary forests and demonstrates how these human-made forests for multiple use were essential for tropical cultures. The same situation was described by Rambo (1979) for the forests of Malaysia. Examples such as these illustrate that use, management and conservation of secondary forests are not independent or even incompatible activities, but in fact synonymous.

Today, there is concern for the destruction of mature tropical forests and the consequences of this destruction to local, regional, and global environments. One of these concerns is the lack of management or control over certain land uses once they are achieved. For example, under traditional practices, most stages of forest development had uses and were managed for those uses. In fact, scientists today advocate mimicking succession with crop plants as one way of increasing the efficiency of human-use of forest resources (Ewel 1986, Hart 1980). This mimicking of succession is itself a mimic of traditional users of tropical secondary forests such as the Mayans and other older, indigenous cultures (Clay 1988).

We have argued that the conversion of mature forests to other land uses including secondary forests is mostly done to satisfy the needs of people opposed to the needs of multinational companies (Lugo & Brown 1982). More recently there have been excellent accounts showing that much of the conversion of mature forests is caused by political, economic and social forces (e.g. land tenure systems, government subsidies, availability of credit, technical assistance, etc.) that have little to do with the satisfaction of human needs (Porras & Villarreal 1986, Schmink 1987). Regardless of cause, the current situation in the tropics, e.g. one of rapid changes in land use at the expense of mature forests, requires intelligent management if this generation of people is to conserve all the values of tropical forests.

Many solutions to the problem of secondary forest management may already be available in the techniques employed by indigenous people (Clay 1988), including the Indian tribes of the Brazilian Amazon (Posey 1982) and the Mayan empire (Barrera *et al.* 1977, Gómez-Pompa 1987). The Mayans did such an outstanding job of forest management that many modern botanists classified their secondary forests as mature (Gómez-Pompa *et al.* 1987). One point of concern in the application of indigenous management techniques today is whether enough yield per unit area can be achieved to support dense populations. Gómez-Pompa (1987) argues that with shifting cultivation the Mayans supported 100–200 people $km^{-2}$ and up to 700–1150 people $km^{-2}$ with intensive agriculture. Today, he points out, the population in the same regions is 10 people $km^{-2}$. However, it is clear that to secure the welfare of tropical people will require a mix of ecosystems and that one cannot advocate absolute preservation of mature forests nor complete conversion to intensively managed systems as the solution to the land management problems in the tropics.

Figure 9 illustrates our concept of the gains and losses, yields and costs, and benefits and tradeoffs to people of the current land-use changes taking place in the tropics. With this diagram we show that people derive benefit from the land conversion process itself and from the various stages of land-use (forests and non-forests). Values, yields, services and costs to humans differ according to the type of land-use produced. Because natural forces will always tend to restore systems to their mature stage, the maintenance costs will increase with increased intensity of management. We believe that people benefit the most when all sectors of the model are active, e.g. when the landscape is most divers and all systems are functional. Therefore, the management strategy should focus on finding out the optimal combinations of all four types of ecosystems (mature, logged, shifting cultivation and intensive agriculture).

To achieve such a balance, it is imperative to manage secondary forests more efficiently. Today, large-scale conversions from mature forests to agricultural lands often take place without full utilization of the resources produced by the conversion process. Interest centres only on the state of a system and opportunities are lost when the process of conversion is not utilized properly. From Figure 9 we identify four areas of lost opportunities for secondary forest management: 1. when forest lands are cleared and burned without utilization of forest products; 2. when the restoration phase of the forest is not properly utilized (i.e. often regarded as a useless land-use); 3. failure to intensify the management of fallow as a tool for reducing the rate of conversion of mature forests; and 4. when land use conversion skips one or more stages (boxes in Figure 9). Each of these lost opportunities will be briefly discussed.

One could argue that the burning of forest products or leaving them in the field when forest land is converted to alternative uses is ecologically sound because nutrients are left on site and eventually returned to the soil. This is true of those conversions for short-term agriculture or other low intensity uses. However, for conversions to intensive land-use where clearing is often accomplished by machines this is not true. This type of conversion simply sacrifices all values of forests without any ecological constraint and seriously compromises the restoration potential of a site. Each step in the conversion of lands has potential useful outputs to people. Efforts are needed to couple people into the conversion process to maximize the efficiency of resource use.

The restoration phase of forests has been used traditionally by indigenous

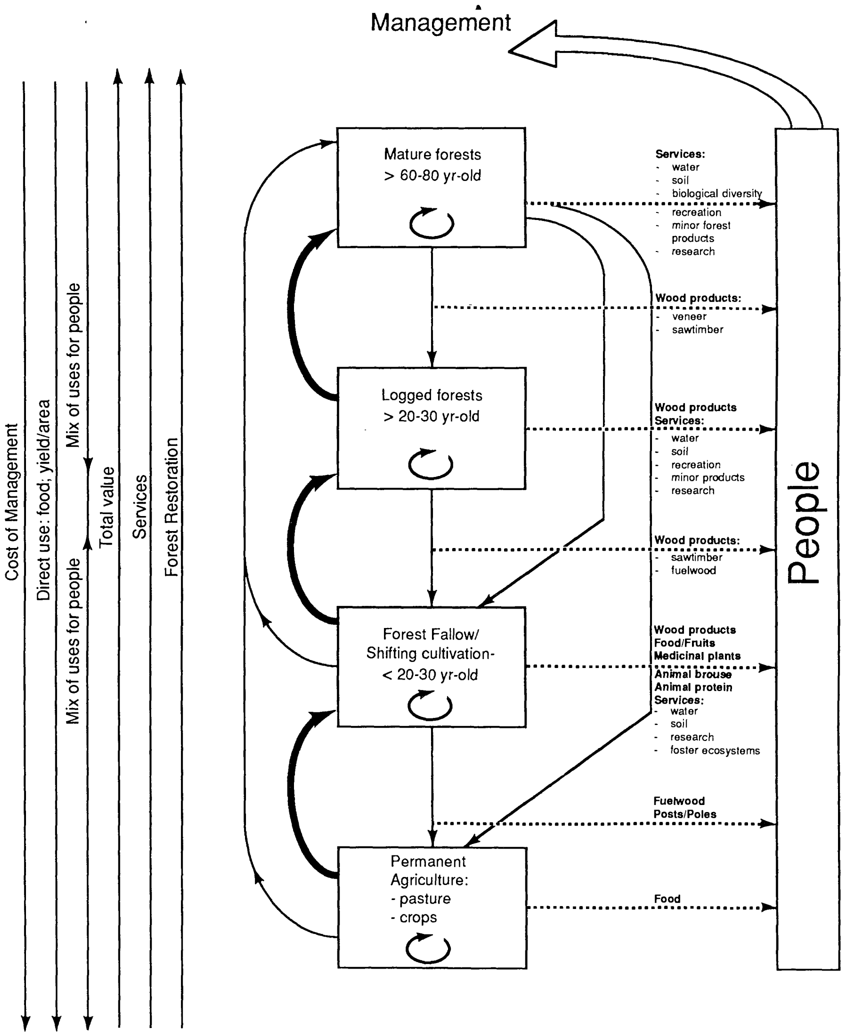


Figure 9. Land-use change in tropical forest lands showing: 1. the conversion of forest lands to other land uses, 2. the products and services (dotted lines) that people derive from the conversion process and the four stages of forest or land use, 3. restoration (arrows on left side of boxes) of forests, and 4. trends in costs and benefits to people from changes in land-use (left side of diagram, trends increase in direction of arrows). Each stage of forest or agricultural land (boxes) can be managed sustainably (shown by circled arrows in boxes), converted to more intensive use (downward arrows), or restored to a more complex forest (upward arrows). Heavy shaded arrows show those restorations most favoured by natural forces. Intensive conversions or restorations may jump over a stage of land-use (boxes) if enough energy is available to overcome costs. Each type of land-use has uniquely important benefits (shown in the trends and listings of products and services) and thus optimal land-use in a landscape requires a mix of all four land-use types.

peoples as an additional source of food, fodder, fibre and amenities (Clay 1988, Denevan *et al.* 1984). Today, many of these technologies are being lost and while secondary forests develop unmanaged, people continue to convert mature forests in search of products and services that could be produced by the secondary forests as they age. Under this heading we advocate use of forests while allowing them to mature naturally. The idea is to grow crops, including tree crops, through perhaps a 30 yr rotation and allow a native understorey to develop so that after the tree crop is harvested, a natural forest takes over and is allowed to mature. These schemes have been described by Hart (1980) and by Ewel (1986).

Closely related to the discussion above is the arresting of forest succession at relatively young stages to take advantage of high yields and reduce pressure on the conversion of mature forests. There are many silvicultural techniques for managing secondary forests (e.g. Wadsworth 1984, Weaver & Birdsey 1986). Wadsworth (1984) suggests four treatment alternatives for improving secondary forest productivity. They are, in increasing order of intensity: 1. no treatment and use for protection (e.g. forest fallow); 2. refining (or timber stand improvement) by reducing competition for promising immature trees; 3. natural regeneration by removing the overstorey to promote seed production and growth of desirable species; and 4. underplanting either as enrichment, gap or line plantings. Weaver & Birdsey (1986) elaborated Wadsworth's scheme for the management of abandoned coffee shade forests.

Each of these techniques has advantages and disadvantages that require careful consideration and a sound data base before application. Also, any intensification of forestry requires an understanding of plant–soil relations to avoid fertility failures after several rotations. These are areas where very little research exists and more is needed. Yet, the only possible solution to the problem of overconversion of mature tropical forests is intensification of secondary and plantation forest management (Wadsworth 1983). Therefore, research in this aspect of forestry is clearly top priority.

When the conversion of forest land is too rapid and land-use stages in Figure 9 are skipped, society loses the goods and services of the lost ecosystem. To avoid such a loss, we advocate management of tropical forest lands with a landscape perspective. This is possible in the tropics where land tenures and development projects are large. Optimal use of secondary forests will occur when: 1. land-use follows a step-by-step intensification assuring coupling of people's needs with use of forest products at each step in the process; 2. sharp increases in intensification are done only under special circumstances, e.g. where conditions assure success; 3. sites optimal for intensification of forest management are arrested in high productive status for several rotations and then released to maturity to allow restoration of long-term productive capacity; 4. sites that do not support intensive management are allowed to mature; 5. opportunities to mimic successions with crops are taken advantage of; and 6. research is closely coupled to management to assure innovation and long-term success of forest use.

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ANNOUNCEMENT

## Reproductive biology of the Orchidaceae: request for information

We intend to review the reproductive biology of the Orchidaceae. To make this review as comprehensive as possible, we are requesting unpublished or soon-to-be published data sets on breeding systems in orchids. The information will be used to make phylogenetic, biogeographic, and growth habit comparisons among species. We are particularly interested in natural levels of fruit set (% of flowers producing fruits) and, where available, results of hand pollinations. Also, any data on seed set (% of seeds bearing embryos) would be useful. To show natural variation in the data, we would appreciate that they be broken down by site and year where appropriate. If the information is already in manuscript form, authors may send manuscripts, indicating to which journal the article has been or will be submitted. Direct information to:

Jess K. Zimmerman

*Smithsonian Environmental Research Center*
*PO Box 28, Edgewater, MD 21037 USA*

Your help will be greatly appreciated and acknowledged.

*Jess K. Zimmerman, Ricardo N. Calvo and James D. Ackerman*

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