

Chapter 3

Primary Forests and Their Productivity

Primary forests are those that have existed without significant human or other disturbances for longer than the lifespan of mature trees (60 to 80 years is used by FAO) (Anon. 1982c). In such relatively stable forests, functional relationships evolve that display preferences, tolerances, capacities, and interdependencies among organisms not otherwise evident. Such forests are self-sustaining and evince both ecological and economic values useful to society. In present times, during a small fraction of the last 2 million years, primary forests are believed to have approached their maximum extent (Whitmore 1982). Many are worth preserving in perpetuity. As a unique source of information on the relations between forests and their environments, primary forests and their dynamics merit thorough study by foresters. They afford important points of reference for assessing silvicultural departures.

This chapter describes those characteristics of primary forests that are significant to productivity. There has been a long history of ecological studies of such forests throughout the Tropics; some of the most thorough were those of Jones (1956) in west Africa and Schulz (1960) in Suriname. More recently, the ecology of wet forests in Puerto Rico (Odum and Pigeon 1970), the Amazon (Fittkau and Klinge 1973), the Far East (Sutton and others 1983, Whitmore 1984), and other regions have been studied.

The physical environment of forest ecosystems determines the pattern and the rate of change, and it may set limits on how far ecosystem development can go (Odum 1969). But the ecosystem itself may in turn modify the physical environment. Succession culminates in a maximum degree of homeostasis in which the ecosystem's organic responses tend to compensate for environmental changes. The primary forest provides maximum self-protection from disturbances. It also attains, relative to available energy, maximum or near-maximum biomass and interaction among organisms. Interaction may include competition, in which one of the organisms involved is suppressed; commensalism, in which one is benefitted, but none is suppressed; and mutualism, in which more than one organism benefits (Longman and Jenik 1974).

Primary forests exhibit both resilience, the capacity to absorb changes and still persist, and stability, the capacity to return to an equilibrium state after a temporary disturbance (Holling 1973).

Compared to other forests, primary forests generally achieve a relatively stable equilibrium between gross production and respiration, low gross production relative to standing biomass, high biomass relative to energy flow, low net production (yield), weblike rather than linear food chains, large volumes of organic matter, intrabiotic inorganic nutrients, high diversity, well-organized stratification and spatial heterogeneity, narrow niche specialization, large organisms, long and complex life cycles, closed mineral cycles, slow nutrient exchange rates with the environment, quality versus quantity production, developed internal symbiosis, and good nutrient conservation and stability (Odum 1969).

Valid as these concepts may be, the traditional vision of the virgin forest as being "unharmed" is unrealistic (Spurr and Barnes 1980). Disturbances (or even major disasters) are natural and frequent relative to the lifespan of most forest trees. Instability of the forest is inevitable, even in the Amazon, where climatic change and tribal intervention may have occurred within the lifespan of the oldest trees. Caution must be exercised in classifying tropical forests as primary because of the possibility of past human intervention (Catinot 1974).

The following description of ecosystems has been adapted from Odum (1972). The structural components include the climatic regime, inorganic substances involved in mineral cycles, organic compounds, autotrophic (self-nourishing) forms of life, and heterotrophic forms (nourished from others). Heterotrophic life forms include phagotrophs, or macroconsumers, which are largely animals that ingest other organisms, and saprotrophs, which are microorganisms that decompose organic matter. The living and nonliving parts of ecosystems are so interwoven that they are hard to separate.

Moist tropical ecosystems are so complex that their performance cannot be studied by traditional one-problem, one-solution investigations. To understand them, it may be necessary to use investigative systems involving mathematical modeling and cybernetics (Odum 1972).

Much recent ecological research may appear peripheral to forest productivity. It concerns information primarily of scientific interest, such as soil microbiota and understory plants, leaf-area indexes, litterfall, biomass, and gross productivity in terms only vaguely indicative of useful wood volume or growth (Harper 1977). Whereas foresters have studied forests chiefly to ascertain how much

usable wood they might produce, ecologists are more broadly interested in how forests function as systems. These broader insights are at least partly of use to the forester. Ecologists have shown the added costs to society of misuse or destruction of forests, and they are explaining phenomena that heretofore were neither well understood nor studied in depth by foresters or anyone else.

The primary forest, an ecological ideal, is not an ideal for production to satisfy all human needs. Evolution tends to favor individual species more than the forest as a whole (Harper 1977). It would be surprising if activity that favored one individual against another also maximized the performance of the population as a whole as a producer satisfying human wants. Thus, production of the entire population requires compensation for some of the evolutionary advancements favoring individual fitness. An example may be the need to reduce forest density to accelerate growth rates of those trees selected for a future timber crop. Such modifications may start with primary forests but, once applied, have removed the forest under such management from the category of primary.

In 1980, the primary and old secondary forests of 76 tropical countries worldwide had an estimated area of more than 6 million km² (Anon. 1982a; table 3-1). They constituted about 76 percent of all potentially productive forests in these countries. In tropical America, the corresponding percentage was 87 percent. Between 1980 and 1990, some 2.4 million ha of closed broadleaf forests were logged in tropical America (Anon. 1993b) suggesting that the area of undisturbed forest in the region in 1990 was about 450 million ha.

Table 3-1.—Extent of undisturbed tropical forests in 1980

Region and no. of countries	Undisturbed productive forest ^a area (thousand ha)
America—33	454,507
Africa—37	118,450
Asia—16	99,033
Total—86	671,990

Source: Anon. 1982e.

^aUndisturbed productive forests are closed primary forests or old secondary forests unlogged for at least 60 years on terrain that could support (without legal objection) production of wood for industry.

Forest Structure

Forest structure is concerned with the sizes, relative locations, and types of life forms. The description presented here applies chiefly to moist forests (fig. 3-1). A summary of structural contrasts between moist and dry, tropical and subtropical primary forests appears in table 3-2 (Murphy and Lugo 1986).

Rain forests, as defined by Baur (1964b), are generally at least 25 m tall. Semi-evergreen forests range up to 40 m; evergreen seasonal forests, to 50 m; and equatorial rain forests from 40 to 60 m. A tall tree reported from a Malaysian tropical forest, a *Koompassia excelsa*, attained 84 m (Foxworthy 1927, cited by Longman and Jenik 1974). Tropical forests tend to be shorter in dry areas and at high altitudes (fig. 3-2). In Venezuela, mean height of trees 10 cm in diameter at breast height and larger at elevations up to 3,000 m above sea level was 10 m; above that elevation, it was 5 m (Veillon 1965).

Forest Density. Forest density is measured by the number and size of the trees, stand basal area, or stocking (volume per unit of land area).

Number and Size of Trees. The number of trees per unit of forest area that have attained a certain d.b.h. is a significant measure of forest density (Schulz 1960). In primary moist tropical forests, the number of trees per unit of area is fairly uniform (table 3-3; Heinsdijk 1957, Wyatt-Smith 1949b).



Figure 3-1.—The canopy of moist forests at low elevations is formed by broad tree crowns, as illustrated by this forest in Panama.

Table 3-2.—Structural contrasts between moist and dry forests

Structural trait	Moist forest ^a	Dry forest ^b
Canopy height (m)	20–84	10–40
Canopy strata (no.)	3 or more	1–3
Leaf area index (m ² /m ²)	5–8	3–7
Uniformity	Uniform	Patchy
Ground vegetation cover	<10%	Low-high
Basal area (m ² /ha)	20–75	17–40
Plant biomass (t/ha)		
Stems and branches	209–1,163	28–266
Leaves	7–10	2–7
Roots	11–135	10–45
Total	269–1,186	78–320

Source: Murphy and Lugo 1986.

^aAnnual rainfall >200 cm; potential evapotranspiration/precipitation ratio normally >1.

^bAnnual rainfall 50 to 200 cm; potential evapotranspiration/precipitation ratio normally <1.



Figure 3-2.—On shallow soils, such as on these limestone hills in Puerto Rico, the forests are short, the trees having low, broad crowns.

The number of trees 10 cm in d.b.h or more per unit of area varies by site. For seasonal forests, the mean is about 500 trees per hectare; for submontane forests, it is up to 1,000 trees per hectare (Baur 1964a). In Venezuela, the number varied with the altitude (table 3-4; Veillon 1965).

In primary forests, most of the trees are small (fig. 3-3). An extensive sampling of the forests of the Amazon (Heinsdijk 1957) revealed that about half the trees are consistently in the smallest class (table 3-5). In higher latitudes, this proportion is lower (Baur 1964a). Stand tables for tropical moist forests show consistency. Dawkins (1959) found great uniformity in tree numbers by sizes in primary tropical high forests and constructed a “pantropical” stand table (table 3-6).

Great numbers of trees start out, but only a few reach large size. Many, of course, are small at maturity. Each tree’s fate depends on its capacity to tolerate or dominate its neighbors, depending in part on the relative capabilities of root systems to obtain water and nutrients and of the crowns to reach adequate illumination.

In large samples of primary forests, the ratio of the number of trees in each diameter class to that in the next smaller class tends to be constant throughout the range

of tree sizes. The de Liocourt quotient, or ratio “q” (Amobi 1973, Harper 1977), is described in the previous chapter. If these ratios are similar throughout the range of diameter classes, the stand is considered “balanced,” because mortality in each class apparently is being offset by a compensating number of trees entering the class from below. If the smaller classes exceed, in number of trees, those immediately larger by a greater ratio than that for the upper end of the d.b.h. range, the stand is considered to be “positive,” in that ingrowth is apparently more than adequate for replacement. A converse trend, termed “negative,” suggests that regeneration may be deficient.

Table 3-3.—Number of trees per hectare in selected tropical forests

Location	No. of trees	
	D.b.h. >10 cm	D.b.h. >25 cm
Guyana	235	— ^a
Ivory Coast	214	— ^a
Malaysia	232	— ^a
Brazilian Amazon		
Madeira-Tapajos	— ^a	12–117
Tapajos-Xingu	— ^a	119–127
Xingu-Tocantins	— ^a	63–121

Source: Heinsdyk 1957, Wyatt-Smith 1949a.

^aNot counted.

Table 3-4.—Trees 10 cm in d.b.h. and larger by altitude in Venezuela

Altitude (m)	No. of trees per hectare
50–600	133
600–1,600	184
1,600–3,000	253
3,000–3,300	189

Source: Veillon 1965.

Moist forests of India are generally balanced (Mathauda 1953), whereas the dipterocarp stands of the Asia-Pacific region are mostly positive, a circumstance of great significance to their culture.

In Africa, a constant logarithmic relation between d.b.h. and tree numbers was found to apply best to shade-tolerant tree species (Jones 1956, cited by Longman and Jenik 1974). With emergent light demanders, however, a deficiency of trees in the middle sizes was common and there was sometimes also a deficiency in small trees. Seedlings of even the most tolerant emergents were apparently not numerous enough to maintain current stocking, surviving only near small gaps in the canopy (Jones 1955, 1956). A bimodal distribution of tree frequencies is not unknown elsewhere (Harper 1977), with dominant and suppressed trees composing the two modes. Baur (1964b) explained the deficiency of trees in the middle



Figure 3-3.—Primary moist forests are typically composed of many small trees beneath a canopy of a few large ones.

Table 3-5.—Distribution of tree sizes in Amazon forests (no. of trees per ha)

Subregion	D.b.h. class (cm)		
	25–34	35–44	>45
Madeira-Tapajos	54–58	30–31	27–30
Tapajos-Xingu	53–55	32–33	31–41
Xingu-Tocantins	33–60	14–29	16–39

Source: Heinsdijk 1957.

sizes by different growth rates, assuming that trees pass through the intermediate sizes more rapidly than through the smaller and larger classes. Jones (1955, 1956) differed, concluding that the scarcity of midsized trees is due to discontinuous recruitment in the past.

Similarly, Schulz (1960) blamed the lack of small trees of *Goupia* in Suriname on historic events that produced irregularities in regeneration. However, he found that at Mapane, mesophytic lowland forests are, as a whole, well stocked with smaller and intermediate-sized trees.

Basal Area. The total basal area of all tree boles (with bark) at breast height per unit of area is a measure of forest density that reflects both tree numbers and size. Even without height measurements, it may be a good index of relative wood volume. In primary moist tropical forests, basal area for all trees 10 cm or more in d.b.h.

Table 3-6.—Approximate pantropical stand table for high forests

D.b.h. class (cm)	No. of trees per hectare
10	247.0
20	101.0
30	42.0
40	20.0
50	11.0
60	7.2
70	4.9
80	3.5
90	2.5
>100	5.4

Source: Dawkins 1959.

Note: High denotes closed primary moist forests.

commonly ranges from 35 to 45 m²/ha, with extremes to 70 m²/ha (Baur 1964a). Basal area may vary with elevation above sea level. A study in Venezuela (for trees 25 cm and more in d.b.h.) showed a mean of 22 m²/ha between 50 and 600 m in elevation, a range from 28 to 31 m²/ha between 600 and 3,000 m, and only 18 m²/ha from 3,000 to 3,300 m (Veillon 1965).

Stemwood Volume. Volume of stemwood—generally based on tree diameters, total or merchantable heights, and some expression of stem taper or form—indicates the potential yield of a forest. For practical purposes, limits must be realistic as to species, minimum stem diameter, and allowances for bark and defects.

Stemwood volumes attained in primary moist tropical forests typically range from 290 to 525 m³/ha (Leigh 1975). For west Africa, a range of 275 to 425 m³/ha has been found (Catnot 1974). The range in Puerto Rico is from 145 to 365 m³/ha; the addition of branchwood to a 2.5-cm limit increases this range to 180 to 440 m³/ha.

Stemwood volume, commonly measured to the 7-cm point, diameter outside bark (d.o.b.), has a relatively constant relationship with total aboveground wood volume, or stemwood plus branchwood (Dawkins 1967). An average of 1.3 as a factor to relate the two is applicable to widely differing forests. The extreme range is from 1.1 to 1.5. Stem and branchwood volume underbark has been found under some conditions to be closely correlated ($R^2 = 0.991$) with the product of tree basal area and total height (Dawkins 1964a).

The product of d.b.h. squared and height gives a good estimation of aboveground tree volume (Dawkins 1961b). For 30 trees of 9 species from the wet mountain forests of Puerto Rico, the formula

$$V = 0.0368 + 0.545 (D^2H),$$

where V = volume outside bark, and D = diameter and H = height, both in meters, gave a correlation coefficient of 0.986, or a practical form factor of 0.6 D^2H . For some forests, a form factor of 0.7 may be closer. In Thailand, a good logarithmic relationship was found between the product of the d.b.h. squared and total height and the dry weight of the stem (Kira and Ogawa 1971).

The relation between stand basal area and stemwood volume is dictated largely by stem height. In Puerto Rico, this relation was found to vary from 6.2 to 7.0 m³/m² for

primary moist forests of basal areas between 20 and 40 m²/ha (Odum and Pidgeon 1970). In Venezuela, the relation varied with elevation, averaging 8.7 m³/m² for stands at 50 to 600 m in elevation, 9.7 m³/m² at 600 to 1,600 m, and back down to 7.4 m³/m² from 1,600 to 3,000 m (Veillon 1965).

Biomass. Recent interest in biomass as a measure of the forest resource can be attributed to three main causes (Parde 1980): (1) increased production of fiber and wood-based panel products, which are more appropriately measured in weight than in volume; (2) increased interest in the biological productivity of forest ecosystems, using dry-weight biomass as a measure; and (3) increased interest in wood energy and chemicals with the approaching scarcity of fossil fuels.

Many life forms other than trees make up biomass. Woody lianas and “stranglers” (trees that attach to other trees for support) are common in primary forests of both wet and dry climates. Other common forms include hemiepiphytic plants (plants that start on another plant), epiphytes, insectivorous plants, and geophytes. All of these are more abundant in wet climates. Biomass also includes animal life, a commonly undervalued component of tropical forests.

Unfortunately, the term biomass is not always used in the same sense, and comparisons of various biomass studies must be made cautiously. Total biomass is only partially phytomass, that portion that is plant tissue, living or dead. Although the term biomass refers to organisms both above and beneath the soil surface, difficulty in measuring or using subsurface material gives rise to the common practice of assessing only aboveground biomass. Biomass may be expressed in terms of either fresh or oven-dry weight, preferably the latter. Two variables are critical to conversions from volume to biomass: the specific gravity of the woods and their moisture contents. Oven-dry specific gravities range from 0.2 to at least 1.3 and vary by both species and site; an overall average for all woods in wet forests is possibly 0.6. Green moisture contents of woods in forests in Colombia and Panama were found to range from 48 to 67 percent (Golley and others 1975). A study of 59 species in Puerto Rico showed a range from 37 percent for *Bucida buceras* to 242 percent for *Ceiba pentandra* (Longwood 1961).

A controversy concerning the measurement of forest growth in terms of phytomass (weight) was reported in the Soviet Union, now Russia (Dylis 1971). Such a

measurement was seen to reflect the demand for forests only indirectly, as systems transforming radiant energy, air, water, and minerals. Forest resources are also characterized by volume, surface, inner structure, chemical composition, and energy content. In Russia, phytomass in secondary broadleaf forests may be only one-half to two-thirds that of primary, mixed, broadleaf-spruce forests. Yet, the secondary forests are more useful to humans because more of the phytomass is in the trunks of the trees (Dylis 1971). Total biomass, oven-dry, for primary, lowland, moist, tropical forests ranges from 300 to 1,000 t/ha. For moist subtropical forests, it ranges from 400 to 450 t/ha (Bazilevich and Rodin 1966, Fittkau and Klinge 1973, Young 1976). The range is 60 to 100 t/ha for moist savannas and 30 t/ha for dry savannas.

Near Manaus in the Amazon Basin, where annual rainfall averages 180 cm, aboveground fresh-weight phytomass of a primary forest plot was found to be about 1,000 t/ha; an additional 280 t/ha was belowground (Fittkau and Klinge 1973). Animal biomass totalled only 0.2 t/ha, of which half was soil fauna.

Common formulas used for tree volume measurement can be adapted to give weights (Crow 1978). Examples are $V = a + bc^2$ and $V = ac^b$, in which a and b are constants and c is the d.b.h. (Parde 1980). For entire stands, using 5 to 10 carefully selected mean trees may be adequate. Their mean biomass may be multiplied by the total number of trees in the forest. Another method is to cut, dry, and weigh the biomass of representative forest samples and then apply the total per hectare to an entire area. Also, an array of trees of different diameters (30 or more) may be weighed to produce regression and mass tables comparable to those commonly used for volumes.

Stratification. Primary tropical forest ecosystems are complex vertically as well as horizontally. The trees and other plants, as well as the animals, may be vertically stratified. Stratification of plants seems best expressed in terms of their height at maturity, because in any one location, stratification may be obscured by the presence of immature trees. Five or more strata have been recognized in some tropical forests versus two or three in Temperate Zone forests (Richards 1952). One explanation is greater light partitioning in a tropical forest made possible by a high canopy, long growing season, and more intense sunlight because of the greater mean angle of incidence (Terborgh 1973). Other postulated explanations for and results of stratification in tropical forests (Smith, A. P., 1973) include the following:

1. Optimal use of light because leaf strata separated vertically by 50 to 70 times the diameter of the upper leaves enable lower plants to escape umbras (shadows)
2. Increased photosynthesis because openings between strata make more carbon dioxide available
3. Better pollination or seed dispersal because flyways are created between strata for insects, birds, and bats
4. Intensified selectivity and interdependence among species
5. Isolated emergent trees or groups that produce an irregular upper surface of the forest canopy, contributing to the ventilation of crowns and favoring high leaf area for the capture of more energy and water than is possible with smooth canopies

Whitmore (1981) drew attention to an appearance of stratification resulting from gap regeneration, which produced adjacent groupings of pioneers, second-generation species, and mature groups.

Horn (1971) pointed out that because only 20 percent of full sunlight is needed for tree growth, strata separated by adequate heights can coexist without unduly interfering with one another. Conceivably, they could photosynthesize twice as much as a single stratum. To be efficient, single-stratum leaves must be distributed regularly without overlap.

The number of stories in vegetation may be related to moisture and soil quality. As conditions become less favorable, there are fewer stories (Baur 1964a). An extreme case is mangrove, which commonly has but a single tree story.

Tree strata are not always recognizable. Leigh (1975) concluded that stratification exists but is impossible to distinguish objectively. Schulz (1960) regarded the classification of stories in the moist forests of Suriname as arbitrary. Baur (1964b) concluded that strata are generally discontinuous, rising beneath gaps.

To expect sharply defined strata to be clearly visible in all parts of the forest is to deny continuous regeneration of trees of all species. To conclude that strata do not exist because of the differences from place to place resulting from gap recovery seems an opposite extreme. Whatever

their practical significance, strata appear to exist in most closed tropical forests if Newman's (1954) criteria for their definition are accepted: (1) omission of immature trees of higher strata, (2) tree maturity defined by no more lateral branches being shed, and (3) height of stratum considered to be that of its lower limit of permanent branching.

Richards (1983) felt that objectively demonstrable or purely arbitrary divisions of a continuum are both oversimplification. He found that mixed rain forest strata are not usually evident, although there are sometimes large numbers of trees in certain height classes. The boundaries between strata are mostly arbitrary and cannot be objectively defined. Richards concluded that it is more important to recognize foliage density variation at different levels. Foliage density is greatest in the understory.

Notwithstanding the difficulties in identifying tree strata, Baur (1964b) ascribed numbers of stories to most tropical forests. For equatorial rain forests, he listed no emergent layer but three or more tree stories and two shrub layers. For evergreen seasonal forests, he listed emergents plus three tree stories. For semi-evergreen and submontane rain forests, he listed two or three stories and in xeromorphic and swamp forests, two stories.

Five strata have been identified in primary forests north-east of Manaus, Brazil (Klinge and Rodrigues 1973). Data on their heights and fresh-weight phytomass appear in table 3-7.

Jones (1956) concluded that 21 percent of the emergent species in the rain forests of Nigeria are very strong light

demanders, scarcely represented in the lower stories. Another 45 percent are abundant in the lower story but scarce in the middle story. About 32 percent decrease in abundance from the lower story to the emergent layer. Other data from Nigeria (Kio 1979) show that two-thirds of the volume of old-growth moist forests is below the upper story. This represents an incompletely tapped reservoir of wood that might be put to use.

Tree Form. Sharma (1976) examined the phytomass of trees by parts for *Buchenavia lanzan* and *Shorea robusta* in India's dry deciduous forests. In these relatively small trees, the proportion of branchwood was significantly greater in the larger size class (table 3-8). Other relationships were variable, although the bole contained more than half the total mass for all sizes.

Root Systems. The root system's portion of total tree phytomass in primary forests evidently varies with local conditions. One study worldwide indicated that roots constitute from 19 to 23 percent of the total biomass (Bazilevich and Rodin 1966). Yet, in one lowland, mixed dipterocarp forest (dominated by trees of the Dipterocarpaceae family) of Malaysia, roots made up only 7 percent of the dry weight of the trees, or 65 t/ha (Brunig 1967). In one of Cambodia's evergreen seasonal forests, roots were found to make up 16 percent of the tree phytomass (Hozumi and others 1969). In evergreen seasonal forests on terra firme near Manaus, Brazil, this percentage was 27 percent (Fittkau and Klinge 1973, Klinge and Rodrigues 1973). In dry climates, trees may develop more extensive root systems (Kozlowski 1982). Four types of root systems of dicotyledonous trees are recognized by Longman and Jenik (1974): (1) thick, horizontal roots commonly merging into large spurs or "buttresses", no taproot, (2) the same, with a taproot, (3) weak surface roots and a prominent taproot, and (4) numerous aerial "stilt" roots and a network of weaker, underground roots. Large, thick roots apparently provide both anchorage and nutrient transport, and the primary function of fine feeder roots is absorption of nutrients and water. In a Latosol near Manaus, 25 percent of the fine roots were found in the litter layer at the surface (Klinge 1973).

Conspicuous tree buttresses distinguish moist tropical forests from most Temperate Zone forests (Leigh 1975). Buttressing and "stilt" roots are especially common in swamp forests and mangroves. Buttressing is most common on upper story trees, but stilt rooting may occur anywhere. Buttressing is less common in subtropical

Table 3-7.—Tree strata and phytomass, Manaus, Brazil

Stratum height (m)	Fresh phytomass	
	Mean weight (t/ha)	Percentage
24-35	190	28
17-26	400	58
8-14	77	11
4-6	16	2
2-3	5	1
Total	688	100

Source: Klinge and Rodrigues 1973.

Table 3-8.—Percentage of phytomass by tree components for two tree species in India

D.b.h. (cm)	Percentage of total weight				Total fresh weight (kg)
	Roots	Bole	Branches	Leaves	
<i>Shorea robusta</i>					
3-6	18	66	10	6	6
13-16	22	66	7	5	77
22-25	22	54	19	5	291
<i>Buchenavia lanzan</i>					
3-6	25	59	6	10	5
13-16	12	75	8	5	53
22-25	11	54	30	5	184

Source: Sharma 1976.

forests at low temperatures (Baur 1964a). Although buttresses would appear to increase stability, their function has not been clearly demonstrated (Longman and Jenik 1974). A form of aboveground rooting common to moist forests is found on stranglers.

Stems. In terms of mass, stems are the largest tree component. In a primary forest near Manaus, the stems made up 50 percent of the total weight of the trees and 68 percent of the aboveground weight, or about 295 t/ha, dry weight (Fittkau and Klinge 1973, Klinge and others 1975). In the subtropical wet forests of Puerto Rico, stems may make up 58 percent of the total tree weight and 77 percent of the aboveground weight (Ovington 1972). In Cambodian evergreen seasonal forests, the corresponding percentages were 56 and 67 percent, or about 135 t/ha, dry weight. In the low miombo woodlands of Katanga, in what was formerly Zaire, the stems made up only 44 percent of the aboveground tree weight, an indication of the shortness of the stems and the branchy habit characteristic of trees under dry conditions (Malaisse and others 1972).

Klinge and Rodrigues (1973) measured the aboveground fresh weight of trees in seasonal evergreen forests along the Amazon. For trees in the intermediate layers (4 to 26 m above ground), stems were found to make up 61 to 67 percent. For trees in the layer between 24 and 35 m above ground, stems made up 73 percent. The stems of most trees in moist tropical forests are columnar and generally straighter than those of broadleaf trees in Temperate Zone forests (Leigh 1975). In a hectare of evergreen forest near Manaus, at least 75 percent of the trees

had more than 8 m of straight stem, and nearly 10 percent had 16 m or more (Prance and others 1976). Taper is also less than in many other forest types (Baur 1964a). Taper measurements from a mixture of posts from wet forests in Puerto Rico yielded the following mean values:

Mid-Diameter (cm)	Stem	Mean taper (cm/m)
10		1.1
20		1.4
30		1.7
40		1.9
50		2.2
60		2.5

Bark weight, measured in a mixed dipterocarp forest, was found to make up 14 percent of the total weight of the trees, or about 120 t/ha, oven-dry (Brunig 1967). Bark-thickness measurements of the stems and branches of 434 trees of 41 different tree species of subtropical wet forests in Puerto Rico showed a mean of 0.6 cm for stems 10 cm in diameter, 1.3 cm for stems 30 cm in diameter, and 1.4 cm for stems 60 cm in diameter. For stems alone, the average was 2.0 cm, with a maximum of 4.8 cm.

Branches. Branch weight varies greatly with tree height. In the evergreen forests of the Amazon, branches were found to make up about 128 t/ha, dry weight, or 21 percent of the total fresh weight of the trees and 29 percent of their aboveground weight (Fittkau and Klinge 1973, Klinge and others 1975). In evergreen seasonal forests in Cambodia, the corresponding percent-

ages were 26 and 31 percent (Hozumi and others 1969). In the relatively dry miombo forests of what was formerly Zaire, the branches made up about 54 percent of the aboveground weight (Malaisse and others 1972).

Crow (1978) found similarity in the stem and branch weights in trees relative to d.b.h. times tree height from wet forests in Puerto Rico and Thailand. He found that the natural logarithm of oven-dry branch weight was equal to a coefficient b times the natural logarithm of d.b.h. squared, in centimeters squared, and tree height in meters, minus a constant c . He found b and c to be similar for these distant forests, 1.050 and 5.521 respectively for Puerto Rico, and 1.027 and 5.116 for Thailand.

The proportion made up by the branches varies not only with tree size but also with strata. In seasonal forests along the Amazon, the proportion of aboveground tree weight in branches was 26 percent in the top layer (24 to 35 m), 31 to 34 percent in the 8- to 26-meter stratum, 23 percent in the 4- to 6-meter stratum, and 15 percent in the 2- to 4-meter stratum (Klinge and Rodrigues 1973). The ratio of branch weight to stem weight is significant to forest utilization. For evergreen forests near Manaus, the ratio was about 0.43 (Fittkau and Klinge 1973, Klinge and others 1975). But it varied among the five tree stories, ranging from 0.35 to 0.56, the highest ratio again occurring in the middle story, between 8 and 14 m above ground (Klinge and Rodrigues 1973). In the evergreen seasonal forests of Cambodia, the ratio was 0.46 (Hozumi and others 1969); in Thailand's forests, it averaged 0.29 (Ogawa and others 1965). In the miombo forests of Africa, branch weight was found to be 123 percent of the stem weight, reflecting the branchy form of the trees there (Malaisse and others 1972).

Tree Crowns. The size and shape of tree crowns influence tree productivity. The trees in the top story tend to have shallow, horizontal crowns; those in the understories have deep, vertical crowns. Zavitkovski and others (1974) conclude that in the Temperate Zone vertical extension of crowns is important to productivity, suggesting the use of Assman's (1970) crown fullness ratio (crown width to crown height) as an indicator. Crown diameter to d.b.h. ratios (Assman's growing-space index) are also significant to growth rates. In the Tropics, these ratios range from about 14 to 28; high-yielding species typically have crown diameter to d.b.h. ratios of 15 to 20; lower yielders have ratios of 25 or more (Dawkins 1963a). Assman (1970) found that the ratio of crown diameter to d.b.h. is greater for suppressed than for

dominant trees; he also noted that it declines with age. Dawkins (1963a) concluded that in the Tropics as well, the ratio declines with age for shade bearers but that strong light demanders may retain a nearly constant crown diameter to d.b.h. ratio throughout life.

For many tree species of New Guinea, the ratio between d.b.h. and crown width in rain forests proved to be nearly linear, ranging between 21 and 23 (Paijmans 1970). A ratio of 22 was found for mora in Trinidad (Bell 1971) and for a group of 15 tree species in Puerto Rico (Wadsworth and others 1989). Large crown diameter to d.b.h. ratios (up to 40) are thought to explain the low volumes of timber per unit of land area produced by huge trees occurring in groups in Africa (Catnot 1974).

Foliage. Foliage makes up 2 to 5 percent of the total biomass in tropical forests (Bazilevich and Rodin 1966, Brunig 1967, Fittkau and Klinge 1973, Hozumi and others 1969, Klinge and others 1975). Leaf weight varies sharply with height above the ground. Near Manaus, Brazil, leaf weight was found to make up 1 percent of the aboveground weight of the trees in the top story, 24 to 35 m in height (Klinge and Rodrigues 1973). In the second layer, from 17 to 26 m, the leaves made up 2 percent. In the third layer, from 8 to 14 m, the proportion was 6 percent. In the fourth layer, from 2 to 3 m, it was 46 percent.

Leaves in primary evergreen forests weigh only 3 to 4 percent as much as the accumulated wood (Brunig 1967, Fittkau and Klinge 1973). However, the annual production of leaves in such forests is about equal in dry weight to the new wood produced each year (Jordan 1971a). In contrast, in Temperate Zone forests, in contrast, wood production reportedly exceeds that of leaves by 50 to 60 percent.

Leaves are the center of photosynthetic activity or productivity. Leaf area is commonly expressed relative to ground area in the same units: the leaf-area index. Studies in the Temperate Zone indicate that there is an optimum leaf-area index; productivity suffers when the index is either above or below that level (Zavitkovski and others 1974). Leaf-area indexes in primary forests range from 7 for seasonal forests to about 12 for rain forests, with extremes to 22 (Golley and others 1975, Hozumi and others 1969, Kira and others 1964). Tropical forests demonstrate similarity of leaf form and size among otherwise unrelated plant families (Leigh 1975). Leaves with entire margins and acuminate tips are prevalent in

moist forests. The average length of the leaves ranges from 7 to 13 cm, and the area from 20 to 180 cm². Light-demanding, opportunist species in rain forests, such as *Ochroma* spp. and *Cecropia* spp., produce exceptionally large leaves. Leaf size decreases in the cool mountain areas (Baur 1964a). Compound leaves are most common in dry forests or the exposed, upper strata of moist forests. In the rain forests of Suriname, about 25 percent of the trees in the top layer have compound leaves (Schulz 1960).

Four patterns of leaf phenology in tropical trees have been distinguished (Longman and Jenik 1974): (1) leaf-fall before bud-break, the entire tree remaining leafless or nearly so for a few weeks to several months; (2) leaf-fall associated with bud-break; (3) leaf-fall completed well after bud-break; and (4) continuous production and loss of leaves.

Deciduousness, characteristic of the first three patterns listed above, may be absent or rare in rain forests (Baur 1964a). In evergreen seasonal forests, as many as a third of the trees may be deciduous, and in semi-evergreen forests, as many as a half. Deciduousness appears to be partly genetic in that the phenomenon is characteristic of some genera (*Ceiba* and *Andira*) regardless of climate. It is also partly environmental in that the timing, degree, and length of the leafless period may vary with current weather.

A relation between the percentage of deciduous trees in the forest and the number of dry months (rainfall in millimeters less than twice the temperature in degrees Celsius) was found in Venezuela (Veillon 1963). With 1 dry month, deciduousness was 20 percent; with 3 dry months, 53 percent; with 5 dry months, 81 percent; with 7 dry months, 88 percent; and with 9 dry months, 93 percent. Other adaptations that reduce desiccation include reduced number and size of leaves, sunken stomata, rapid stomata closure, and leaf waxes (Kozlowski 1982).

In Sri Lanka, leaf-fall may take place after a period of low humidity and low rainfall; the reflush after high humidity and rainfall (Koelmeyer 1959). Flushing of leaves of 150 dipterocarp species in Malaysia occurs twice each year, in April and October (Ng 1981). In dry forests some trees drop their leaves at times unrelated to the dry season (Madge 1965). One species shed twice a year: once in

the middle of the dry season and once at the start of the wet season. *Alchornea* drops leaves only in the middle of the wet season.

Forest Composition

Composition deals with diversity of species in an ecosystem, measured by richness (the number of species), equitability (their respective representation), and heterogeneity (the dissimilarity in richness and equitability) (Peet 1974).

Diversity. Composition is concerned with the species makeup of the organisms that comprise the forest. A striking attribute of nearly all tropical forests is the large number of species they contain. Of the 3 to 10 million species of organisms in the world, two-thirds are limited to the Tropics, and most of these are forest dwellers (Prance 1982). Possibly 80 percent of the tropical plant species have been named, but less than 50 percent of the insects. In Amazonia alone, there may be a million species of insects. There are more than 50,000 species of higher plants. In a world where major food crops total less than 20 species, the richness of tropical forests suggests an almost completely untapped resource.

The large number of tree species in primary forests of tropical America has been reported by Gentry 1988 and by Gentry and Dodson 1987. In a 0.1-ha plot at Rio Palenque in Peru, the total number of trees, including seedlings, was 653, including 114 different species. Of trees 10 cm in d.b.h. or more, there were 52 individuals and 32 species, or fewer than 2 trees per species. In a 1-ha plot at Yamamono, Peru, the number of tree species was 285, ranking well with the most complex forests of the Far East (Whitmore 1984).

Studies in the evergreen forests of tropical South America have shown great extremes in numbers of tree species. In 0.1-ha plots in several forests of Suriname, the average number of species of trees 10 cm in d.b.h. and larger ranged from 110 to 120 (Schulz 1960). In a 3.5-ha plot at Castanhal, Para, Brazil, 179 tree species of 10 cm in d.b.h. or more were found; 70 additional species were found nearby (Pires and others 1953). A plot of terra firme forest near Manaus, Brazil, contained 51 tree species of 15 cm in d.b.h. or more on 0.25 ha, 99 species on 0.5 ha, and 179 species on 1 ha (Prance and others 1976). These are the equivalent of one species for every two trees.

Terra firme forest, which makes up about 95 percent of the vegetation along the Amazon (Gachot and others 1953), has been sampled systematically by the Food and Agriculture Organization (FAO). The FAO's inventory of Amazon forests (table 3–9) consisted of a series of east-west transects more than 3,500 km in length and 1,200 ha in area (Glerum 1960; Heinsdijk 1957, 1958a, 1958b, 1958c).

The tree species of evergreen tropical forests are not only numerous but also taxonomically diverse. Of all botanical families, 72 are composed essentially of tropical trees (Baur 1964a). Of these, 16 are found in all 3 tropical forest regions: Africa, America, and Asia-Pacific. Another 32 are in 2 regions, and 24 are confined to 1. Many genera also are represented in two or three regions. One species, *Ceiba pentandra*, is found in all three regions, presumably as a result of the mobility of its seeds.

In the American Tropics, genera with large numbers of species include the following:

Genus	Family	No. of species
<i>Miconia</i>	Melastomataceae	700–900
<i>Myrcia</i>	Myrtaceae	500
<i>Guatteria</i>	Annonaceae	250
<i>Inga</i>	Fabaceae	200–250
<i>Psidium</i>	Myrtaceae	150
<i>Coccoloba</i>	Polygonaceae	125–150
<i>Cecropia</i>	Moraceae	120

In the extensive FAO transects in the Amazon Valley, three botanical families predominated in trees > 25 cm in d.b.h. (table 3–10; Heinsdijk 1960). Despite the 3,500-km, east-west spectrum of the samples, most botanical groups show no marked preference for either end of the transects. A few that are best represented at the

western end, in the central Amazon, are Celastraceae, Eleocarpaceae, Melastomataceae, Moraceae, Myristaceae, Nyctaginaceae, Olacaceae, and Vochysiaceae. Genera apparently more common in the lower Amazon include *Eschweilera*, *Manilkara*, *Micropholis*, and *Vouacapoua*.

Fanshawe (1952) described two forests dominated by single species in Guyana, one a type of rain forest dominated by greenheart (*Ocotea*) and the other, on white sands, dominated by wallaba (*Epirua*). Both species regenerate abundantly. They illustrate a marked tendency for single species dominance of forests on adverse sites such as these white sands (Schulz 1960). Mangroves are, for the same reason, also forests of limited diversity, composed almost entirely of one or two tree species (van Steenis 1958).

Dominant tree species tend to be: (1) well adapted to the site, (2) fairly frequent and heavy seeders, (3) relatively shade tolerant in youth, (4) capable of taking over gaps, (5) tall, and (6) fairly dense in crown (Baur 1964a).

Dominance of one or a few tree species in rain forests is more common than may be generally realized. In most rain forests, the recognition of forest types or other units depends largely on the behavior of a few key species. Species that are ecologically dominant are not always indicator species for the classification of rain forests (Baur 1964a). Ecologically dominant species, however, may be directly related to occurrence of economically important species.

The final composition of an undisturbed forest community can be ascribed to both opportunity and competition, the former selecting among the potential pioneers, the latter establishing a dynamic balance in structure and pattern (Poore 1964). One view of the rain forest is that it is a continuum of species, each with different tolerances (Schulz 1960). There may be sharp differences at the ends of a spectrum, but none in between. The concept of a continuum that is uniform may be as impossible as that of a discreetly distinct association.

The natural distribution of a plant species is not solely a response to physical conditions prevailing in the habitat. In the Tropics, competition more than physical environment controls selectivity of organisms (Dobzhansky 1950). Plants can normally exist far beyond their natural distribution areas if they are protected from competition. The natural distribution limit of a species is where (as a

Table 3–9.—No. of tree species >25 cm in d.b.h. per unit of terra firme forest in the Amazon

Subregion	10-ha unit	50-ha unit
Madeira-Tapajos	141–150	192–200
Tapajos-Xingu	100–118	142–198
Xingu-Tocantins	121–126	157–171
Tocantins-Guama/Capim	118–124	156–178

Source: Heinsdijk 1957, 1958a, 1958b, and 1958c.

Table 3-10.—Percentage of all trees >25 cm in d.b.h. by family in the planalto Amazon forest

Family	Location			
	Madeira-Tapajos (Central Amazon)	Westbank of Rio Tapajos	Westbank of Rio Xingu	Tocantins-Capui (Lower Amazon)
Burseraceae	4.2	7.0	6.0	6.1
Lauraceae	6.6	7.0	4.2	1.9
Lecythidaceae	11.5	14.5	15.2	25.8
Leguminosae	17.7	21.8	21.1	18.9
Moraceae	5.0	6.5	3.4	2.2
Myristicaceae	4.0	6.1	2.2	0.8
Rosaceae	7.0	1.1	5.8	6.4
Sapotaceae	12.8	9.2	19.7	18.4

Source: Heinsdijk 1960.

result of changing physical environmental factors) its capacity to compete is so reduced that it can be ousted by other species (Walters 1973).

Species in the same community occupy different ecological niches or specific habitats and seldom compete directly in all respects. Gause's (1934) exclusion principle states that two or more species with precisely the same living habits and requirements cannot coexist indefinitely in the same habitat because one will inevitably prove more efficient and crowd out the others. Nevertheless, each species apparently does not require a totally distinct physical niche. Species that superficially look much alike may differ in many less obvious characteristics such as lifespan, growth rate, tolerance, reproductive strategy and mechanism, phenology, and seed dispersal (Richards 1969).

Evolution tends toward digression from similar niches (Whittaker 1965, 1970). Ashton (1969) called this process "mutual avoidance." He concluded that it has reduced the gene pools of the constituent species of stable primary tropical forests but has also led toward morphological stability.

An explanation for the large numbers of tree species in tropical forests is complex. It is no longer thought due simply to the generally favorable environment for plant growth, with few extremes of either temperature or moisture. One theory was that the "low competitive nature" of such a "permissive" environment (Baker 1970b) would favor the survival of mutant forms and, thus, create diver-

sity (van Steenis 1969). For the same reason, the species extinction rate was presumed to be low. Not only is the degree of competition assumed by this argument questionable, but there is reason to believe that a permissive environment might not have stimulated evolution of the species already present.

The role of predators in preventing domination by a few species (and, thus, favoring coexistence for many) has been expounded persuasively by Janzen (1970a) who studied tropical forests of both hemispheres. Yet, many are reluctant to view the animal component as a powerful selective force in plant evolution. Janzen postulates that the wealth of the lowland tropical flora and the relatively long distances between trees of the same species result in part from the action of predators on seeds and seedlings. He points out that any event that increases the efficiency of predation on seeds and seedlings of a given tree species may reduce the population of the adults of that species or increase the distance between new adults and their parents. Either condition will lead to a larger number of species by preventing the best competitors from becoming common enough to eliminate the others. Janzen's explanation, however, is not borne out in all cases.

Species richness (diversity) has its origin in ancient history. Speciation has been in progress ever since the continents separated. In the Amazon (and in Africa as well) climatic changes as recent as 1,500 years ago produced a drier and cooler environment that favored only isolated patches of forests. New species probably evolved in

these isolated areas and increased species richness with long lifespans. Woody vines and a rich shrub flora may also have developed (Budowski 1965).

Primary tropical moist forests are rich partly because coevolution and succession have progressed to a point of relative stability in which species take advantage of interdependency with others. The major tree species, unlike those of secondary forests, are shade tolerant, especially in youth, and have long lifespans.

Ecosystems with many species are generally found in environments with little climatic fluctuation over time. Such has been the case in the humid Tropics and sub-Tropics (Stern and Roche 1974) since the Cretaceous period (Baker 1970b), and these regions largely escaped glaciation (Longman and Jenik 1974). Ashton and Brunig (1975) point out that there were some climatic changes during the Pleistocene era, especially in Africa and the neotropics, but there remained refugia for humid forests. This observation leads to the presumption that most of the species have evolved to a high degree of competitiveness. The past stability of the Tropics, according to Connell and Orians (1964), allows energy that would otherwise go into regulation of the climate to be used for more productivity, larger populations of organisms, more opportunities to form interspecific associations, and greater genetic variety.

The length of time an environment has remained stable affects the development and regulation of niches, most of which result not from variation in the physical environment but from interactions among organisms (Connell and Orians 1964). Ashton (1969) concluded that seasonal and geological stability has led to selection for mutual avoidance, increased specialization, many (but narrow) niches, and integrated systems of high productive efficiency.

Functional adaptations contribute to the coexistence of so many species. Examples are sequential specialists (those with seasonal functional strategies), interstitial species (those dependent on fringe areas between high densities of other species), and hypercontingent species (those dependent directly on relationships between at least two other species) (Colwell 1973). A small increase in the number of niches so developed might make a large difference in the number of species accommodated (Stern and Roche 1974).

Diversity may be manifest in a number of dimensions, such as microsites within a habitat, polymorphism, groupings at levels higher than species, genetic variants within species, and age (Harper 1977).

Ashton (1969) saw difficulties in relating forest composition to any specific cause. He concluded that each rain forest tree occupies a succession of microhabitats during its lifespan; therefore, it is impossible to determine whether a particular tree arrives at maturity through a process of selection, by means of a complex series of competitive hurdles alone, or in part by chance. He assumed that all three are involved and that the relative importance of each will vary, although selection always plays a crucial part.

A good discussion of the hypotheses regarding diversity and adaptive strategies in rain forests was presented in Spanish by Toledo (1976). He emphasized a need to study life cycles of more species.

An analysis of Costa Rican forests suggests that species richness does not increase with available soil nutrients; in fact, the relationship may be just the opposite (Huston 1980). Tree-species richness was analyzed in 0.1-ha plots; the significant soil nutrient parameters were phosphorus (P), potassium (K), calcium (Ca), sodium (Na), total bases, base saturation, and cation exchange capacity. No significant relation was found for available nitrogen (N), total N, organic matter, manganese (Mn), or magnesium (Mg). Correlations with precipitation, tree density, tree height, and soil fertility suggested that within the range of the 46 sites studied, the greatest tree richness occurs under poor conditions.

Whitmore (1982) postulates that the forests richest in species are those recovering from a major disturbance, in that they contain both pioneers and their successors. This is the intermediate disturbance hypothesis of Connell and Orians (1964). Disturbances of some degree are considered continuous, enabling both mature forests and all other stages to coexist (Orians 1982). Within such a mixture, there is much duplication in species tolerances.

Species diversity has commonly been considered a measure of ecosystem stability (Stern and Roche 1974). In the gross sense, there is an element of truth in this, because diverse systems of the Tropics are adapted to maintain themselves in a relatively stable environment. The

rapidity with which cleared areas naturally reforest may be positively related to former species richness. However, if stability is to be taken literally, diversity and complexity beget fragility rather than stability. The probability that disturbances will greatly affect food chains, intrabiotic nutrients, biochemical diversity, spatial heterogeneity, mineral cycles, and internal interdependencies is far greater in complex ecosystems than in simple ones.

Diversity has been a powerful obstacle to the exploitation of mixed tropical forests. The percentage of tree species of commercial interest in the past has been low, and even among these, the percentage of merchantable stems (at least for lucrative export markets) has been even lower. In the rich forests of Borneo, for example, as recently as 1967, utilization was but 45 t/ha, or only 7 percent of the aboveground wood volume and 5 percent of the biomass (Brunig 1967).

Population growth within the Tropics and expansion of local markets have markedly increased the proportion of harvestable industrial wood in some areas. Carton de Colombia (Frisk 1979), for example, has utilized up to about two-thirds of the wood volume (100 species) of its mixed forests for a variety of products, including cellulose.

Species diversity is commonly expressed by the number of species per unit of land area: number of species increases as area increases. A crude measure of the "importance" of any species may be expressed in terms of its dominance, density, and frequency (Curtis and McIntosh 1950). Dominance is the proportion of the total basal area; density is the proportion of the total number of trees; and frequency is the proportion of a set of samples within which a species is found. Basal area alone was considered a good single indicator of species importance by Baur (1964a, 1964b), but Schulz (1960) believed it gives too much weight to infrequent dominants. The significance of frequency is seen in data from 2-ha plots in Brazil and Malaysia (Baur 1964a). Of 405 tree species, 166, or 41 percent, were represented by a single tree.

The diversity of tropical forests should be measured by more than the number of species present or even by any special horizontal arrangement of species. Meaningful diversity also includes the relative representation of different species.

Heterogeneity. The existence of a great number of species in the forests of the Tropics is further complicated by heterogeneity, a lack of consistency from place to place. Patchiness in species occurrence and size groups has been reported from all moist tropical forest areas. Described as "discontinuity" among the tallest trees and the herbaceous vegetation and "clumping" among the smaller trees (Fontaine 1976), patchiness has been noted particularly in regeneration, a fact of utmost significance to wood production (Baur 1964a). In Suriname, canopy dominants were observed to occur in groups, with a relatively small number of leading species found in each (Schulz 1960). Many are common among the groups, but species vary in their prominence. Patchiness in different species groups may appear in secondary forests as early as age 12 (Webb and others 1972).

Some observers have concluded that patchiness is largely a result of chance. Early studies in Nigeria indicated that emergent trees were distributed more at random than those of lower stories, and few pairs of a species occurred as common associates (Jones 1955, 1956). Observations in Suriname indicated that variations in forest composition are somewhat accidental but left doubt as to whether mixed forests are purely chance aggregates with no pattern (Schulz 1960).

Later studies in Nigeria supported the purely random theory, because many species were seen as interchangeable (despite Gause's exclusion principle), with similar physiological and ecological requirements (Longman and Jenik 1974).

Other theories for forest heterogeneity are based on intricate microenvironmental variations. Richards (1953), noting that most of the species occur over large areas, suggested that their occurrence might vary locally in response to slight changes in topography, soil, and microclimate. Webb and others (1967) concluded that the floristic composition of Australian rain forests reflects the environment with great precision and found that social cohesion within the forest is more vertical than horizontal. Each species group was seen as a functional system of interacting plants, possibly representing a skeletal ecosystem with its own microenvironment and animal organisms. Studies in Malaysian lowland forests (Poore 1968) suggested that rare species occur in associated groups responsive to soil and microenvironment, but are immersed in a matrix of commoner species with a distri-

bution determined more by chance. Groups of species were seen to occupy distinct habitats, each differing in the narrowness of their tolerances.

Possibly the most plausible explanations of the heterogeneity of tropical forest composition lie in the infinite variety of circumstances that influence reproduction. The fact that such influences might also vary widely with time seems to deepen the mystery. An early and intriguing theory was developed by Aubreville (1948) after long observation in west Africa. Called the "mosaic" theory (Richards 1952), it suggests that only certain species may succeed others, forming a variety of contemporaneous but differing multispecies sequences.

Baur (1964b) saw in the species patchwork a result of the nature of overstory mortality. The death of a single mature tree that remains standing stimulates only gap opportunists, not all secondary species. If the tree falls over, creating a large opening, an even-aged stand of secondary species enters. Poore (1968) concluded that in Malaysian forests the distribution of the common species is determined primarily by relations among flowering, fruiting, dispersal agents, and gap formation.

Longman and Jenik (1974) describe three characteristics of primary forests, following, that tend to confirm reproductive factors as one cause of heterogeneity:

1. Mature stands with an unbroken canopy of large trees, lianas, and vines, with rare grasses and forbs covering only a small proportion of the soil and with seedlings and small trees scattered irregularly
2. Gaps, commonly caused by falling trees, normally covering less than 5 percent of the forest area, with luxuriant development of climbers and ground herbs and with germination of dormant seeds and accelerated seedling growth
3. Thickets, resulting from a former gap, with dense, tangled masses of living and dead climbers, low light intensity beneath, and no herb layer.

Ashton (1969) concluded that because distribution of tree species within the forest varies with size of recent openings and their proximity to seed sources, single visual counts may be misleading as to the responsible factors. Such counts may merely record the consequences of

historic and catastrophic events and subsequent difficulties in the reestablishment of certain species, none of which may still be readily discernible.

It is evident then that the wealth of species in tropical moist forests cannot be explained easily. Such wealth is not simply due to an absence of competition, for competition appears to be fierce, probably intense enough to offset the region's favorable environment for rapid plant growth. Indeed, stand basal areas are no greater in tropical rain forests than in Temperate Zone forests. The probability is that during a long period of stability, growing intimacy and interdependency among species have favored diversity.

As with trees, small mammals in tropical ecosystems are unequally distributed among species (Fleming 1975). One to three species are usually dominant, yet the biomass may be concentrated in a few other (not necessarily abundant) species. Rare species make up a greater proportion of the birds of tropical forests than of temperate forests. Mixed moist tropical forests with little environmental seasonality favor extreme specialization in the food habitats of birds (Harper 1977).

Nutrient Cycling

Primary forests are known for large accumulations of organic matter, concentrations of several nutrients primarily within the biota, closed nutrient cycles, slow rates of nutrient exchange between organisms and the environment, and good nutrient conservation (Odum 1969). These attributes generally contribute to stability, which underlies sustained production.

Nutritive elements can be classified into three groups: nonmetallic—N, P, S, and boron (B); light metals—K, Ca, and Mg; and heavy metals—iron (Fe), Mn, copper (Cu), zinc (Zn), and molybdenum (Mo) (Assman 1970).

Nutrients come from surface and subsurface minerals and from the atmosphere and are loosely held and readily available in humus and clay soil fractions (Assman 1970). In the moist Tropics, the uptake of mineral-derived nutrients by forests may reach 2 t/ha/yr (Bazilevich and Rodin 1966).

The physical and chemical composition of an undisturbed moist forest at Kabo, Suriname, is summarized in table 3-11 (Anon. 1980a). The preponderance of N is

Table 3-11.—Biomass and principal nutrients in an undisturbed moist forest at Kabo, Suriname

Component	Dry phytomass (t/ha)	Nutrient (kg/ha)				
		N	P	K	Ca	Mg
Leaves	10	170	9	112	66	21
Branches	105	532	44	361	542	60
Stems	231	767	53	521	811	115
Roots	26	289	13	122	47	40
Subtotal	372	1,758	119	1,116	1,466	236
Litter ^a	48	365 ^c	25 ^d	45 ^e	227 ^e	59 ^e
Soil organic matter ^b	129	7,869 ^c	20 ^d	113 ^e	173 ^e	83 ^e
Total ecosystem	549	9,992	164	1,274	1,866	378

Source: Anon. 1980a.

Note: N = Nitrogen. K = Potassium. Mg = Manganese. P = Phosphorous. Ca = Calcium.

^aIncludes standing dead wood.

^bTo a depth of 170 cm.

^cTotal N content.

^dP-Bray I: available P.

^eExchangeable cations.

impressive, making up three-fourths of the total phytomass. Also notable is the fact that only 20 percent of the N is in the aboveground phytomass.

Only about 0.3 percent of the world's N is in living organisms, humus, and seabottom compounds (Wollum and Davey 1975). Nearly all the rest, 97.8 percent of the total, is in rocks; only 1.9 percent is in the atmosphere. In the Temperate Zone, the addition of N from the atmosphere to the earth's surface is 4 to 10 kg/ha/yr (Wollum and Davey 1975). Recycling of N, unlike that of other nutrients, may be 6 to 10 times greater in tropical forests than in Temperate Zone forests (Laudelot and Meyer 1954).

Forests obtain N partly from the atmosphere, especially during heavy storms, but chiefly through biological fixation, which is attributed to blue-green algae (in participation with lichens) and bacteria (Wollum and Davey 1975). Such fixation may amount to 20 to 40 kg/ha/yr. Nitrogen is also fixed in moist forests by microorganisms in the phyllosphere, the contact layer between the leaves and the atmosphere.

Better known, however, is the input of N into forests through microbe-root relations of some legumes. Raised

as crops, legumes may fix up to 200 kg/ha/yr of N. The process requires the minerals Mo, Ca, Fe, and Cu. In natural forests, N fixation by legumes has scarcely been studied. One large sample of leguminous plants indicated that as many as 90 percent have nodules, suggesting N fixation but not proving it (Wollum and Davey 1975). In west Africa, leguminous trees are fairly common, but many have no N-fixing nodules on their roots.

Nonleguminous, nodulated plants, both angiosperms and gymnosperms, also exist in tropical forests. Among the angiosperms are 10 families, 15 genera, and 113 species, including *Casuarina* and *Alnus* (Wollum and Davey 1975). Nonleguminous, N-fixing plants are generally less active than legumes.

As a reservoir of total N, the forest floor is more important than the mineral soil. The N content of most surface soils ranges from 0.3 to 0.4 percent by weight, generally decreasing with depth (Wollum and Davey 1975). However, most of the N reaching the soil is probably immobilized by organisms that convert elemental N to forms that are usable by plants but that require N themselves to grow. Thus most of the N in and on the soil is unavailable to plant roots. Much may be tied up in undecom-

posed humus and must undergo changes that release ammonia (Wollum and Davey 1975).

Rainwater both brings and transports nutrients as it passes through the forest, generally carrying far more than it had initially by the time it reaches the forest floor. In a lowland rain forest in Malaysia, 98 percent of the nutrients added by rainfall reached the ground as throughfall and the rest as tree stemflow (Manokaran 1980). How much of these nutrients in solution might be lost is not known, because the water was not assessed below the root zone, where much of the water-borne minerals would probably be absorbed by roots before escaping. Indications of changes in the nutrients carried in rainwater in the La Selva forest in Costa Rica are summarized in table 3-12 (McColl 1970).

A major source of nutrients is recycled litterfall: the leaves, branches, and other dead vegetation that accumulate on the forest floor. Litterfall is thought by some to relate directly to gross productivity. Its amount varies widely from place to place. In Panama, litterfall biomass was found to range from 0.7 to 4.6 percent of the aboveground standing crop (Golley and others 1975). In Costa Rica, 58 percent of the total was leaves, 38 percent branches, and 4 percent flowers and fruits.

In the Western Hemisphere, rates of litterfall range from 7 t/ha/yr for mora forests in Trinidad (Cornforth 1970a) to 10.2 t/ha/yr for Colombian rain forests (Bray and Gorham 1964) and 21.9 t/ha/yr for the Amazon (Stark 1971).

This wide range in litterfall rates may actually reflect differences in forest productivity, but because the rates

seem inconsistent with wetness of climate, there apparently are also differences in the dryness of the litter samples weighed or in the degree to which small branchwood may have been included. The published reports of these studies do not describe methods in sufficient detail to permit direct comparisons.

Litter, whatever its accumulation rate, is critical to the future of the forests. Although plants withdraw nutrients from leaves before dropping them (Tanner 1977), there is a residue of nutrients in litter that is a major source for the ecosystem (table 3-13; Cornforth 1970a, Klinge 1977, Nye 1961). The data in this table are not directly comparable. For example, the Brazilian dry season, although less than half the year in length, may produce more than half of the annual leaf-fall. Relatively high amounts of N and Ca were being recycled in all areas.

Treefall is another significant source of nutrient cycling, although it has been measured less than litter. Tree mortality in a natural forest leads to replacement of over-mature, suppressed, and diseased trees by more vigorous competitors. Tree mortality has been estimated at about 1 percent per year for all tree sizes (Leigh 1975). A life table drawn up for the palm, *Prestoea montana*, shows that less than half the trees 2 m tall make it to 3 m; of those that do, less than a third make it to 4 m; and of those, only 2 percent make it to 12 m (Bannister 1970). Standing dead trees are commonly decomposed by insects and fungi and recycled by nearby tree roots that may penetrate decadent wood before dead trees fall.

Coarse litter of 10 cm in diameter or more, including treefall, may be as significant to recycling as fine litter. In

Table 3-12.—Nutrient changes in rainwater at La Selva, Costa Rica

Location	Nutrient content				
	N (pp/m) ^a	P (pp/m)	K (meq/L) ^b	Ca (meq/L)	Mg (meq/L)
Rainfall	0.110	0.000	0.006	0.008	.010
Throughfall	.220	.030	.018	.013	.007
Stemflow	.980	.104	.050	.040	.006
Soil solution at 8-cm depth	.310	.000	.022	.126	.193

Source: McColl 1970.

Note: N = Nitrogen. K = Potassium. Mg = Manganese. P = Phosphorous. Ca = Calcium.

^aPp/m = parts per million.

^bMeq/L = milliequivalents per liter.

Table 3-13.—Nutrient content of litter in forests of three tropical countries (kg/ha)

Source	Nutrients				
	N	P	K	Ca	Mg
Ghanaian rain forest	199	7	68	206	45
Brazilian seasonal forest (5-month dry season)	56	1	6	14	2
Mora, Trinidad	60	3	11	65	15

Source: Cornforth 1970a, Klinge 1977, Nye 1961.
 Note: N = Nitrogen. K = Potassium. Mg = Manganese. P = Phosphorous. Ca = Calcium.

a mature rain forest in Nigeria, the annual weight of treefall was found to be about 11.2 t/ha/yr, or 6 percent more than litterfall (Nye 1961). Nutrient content of this treefall, compared with that of litterfall, contained per unit of weight only 17 percent as much N, 38 percent as much P, 8 percent as much K, 37 percent as much Ca, and 16 percent as much Mg. This appears to verify that the nutrient content of stemwood is generally lower than that of branches, bark, and foliage.

Rainwash, including throughfall and stemflow, has already been mentioned as a vehicle for the transport of nutrients. In Nigeria, rainwash was found to transport 12.3 kg/ha/yr of N, 3.7 kg of P, 220 kg of K, 29 kg of Ca, and 18 kg of Mg (Nye 1961). In Malaysian rain forests, leaching of K, Ca, and Mg directly from the canopy was found to be a source of nutrients almost as great as litter (Kenworthy 1971). Nye (1961) found that in rain forests in Ghana, significant amounts of P and K may be washed out of the canopy by rain (table 3-14).

Table 3-14.—Nutrient cycling in a Ghanaian rain forest (kg/ha/yr)

Process	Nutrient returned				
	N	P	K	Ca	Mg
Litterfall	159	5.8	54	164	36
Treefall	29	2.3	5	65	6
Rainwash	10	2.9	175	23	14
Total	198	11.0	234	252	56

Source: Nye 1961.

Note: N = Nitrogen. K = Potassium. Mg = Manganese.
 Ca = Calcium. P = Phosphorous.

Losses of certain nutrients from a primary forest ecosystem in Papua New Guinea (table 3-15) illustrate the nutrient conservation capacity of the ecosystem (Turvey 1974). Only a small fraction of available nutrients is being lost to streamflow. If the ecosystem is stable, these losses are presumably being replaced largely from weathering of the substrate.

Litter decomposition in the Amazon is attributed largely to fungi (Fittkau and Klinge 1973), whereas arthropods may be more significant elsewhere (Madge 1965). Termites are ubiquitous and undoubtedly a major factor in litter decomposition throughout the Tropics. Madge considered the earthworms present in Nigerian rain forests to be of little importance to litter decomposition.

Anderson and Swift (1983) questioned the widely held belief that plant litter decomposes rapidly in the humid Tropics and that a major portion of the ecosystem nutrient capital is in phytomass, thus leaving soils with a low organic-matter content. Citing the occurrence of widespread Podzols containing more than 60 percent of the N and P capital in deep humus horizons (Klinge 1966), they question broad generalizations. They conclude that decomposition rates are not purely a function of moisture and temperature and that the relative balance of nutrients and active decay organisms may cause sharp variations from place to place anywhere in the Tropics or Temperate Zone. Three groups of variables (Swift and others 1979) are responsible for these variations: microorganisms, litter quality, and the physiochemical environment (Anderson and Swift 1983).

Under conditions favorable for decomposition, litter accumulates beneath moist lowland forests only after seasonal pulses of leaf-fall. Golley and others (1975) found that in premontane wet forests, litter present in

Table 3-15.—Nutrient losses in a primary forest ecosystem in Papua New Guinea (kg/ha)

Content	Nutrient				
	K	Ca	Mg	Na	Si
Total in ecosystem	7,166.0	237.0	6,233.0	6,981.0	14,684.0
Annual flux					
Rainfall input	0.8	0.0	0.3	8.4	0.0
Streamflow loss	14.9	24.8	51.0	66.0	288.1
Net loss	14.1	24.8	50.7	57.6	288.1

Source: Turvey 1974.

Note: K = Potassium. Mg = Manganese. Si = Silicon. Ca = Calcium. Na = Sodium.

May was more than half gone by November and more than 80 percent gone by February. Exceptions are swamps where decomposition is partly anaerobic and slower than elsewhere and forests at high elevations where lower temperatures slow the process. Under tropical montane conditions, humic topsoil may reach 5 to 10 percent of total biomass (Young 1976).

In Nigerian rain forests, litter decomposed in 4 or 5 months during the wet season, but decomposition was essentially arrested during the dry season (Madge 1965). Early estimates in what was formerly Zaire (Laudelot and Meyer 1954) showed that litter decomposed in miombo and other dry woodlands in 2 to 3 years.

During a 5-month dry season near Manaus, Brazil, the percentages of mineralization were 62 percent for N, 85 for P, 79 for K, 33 for Ca, and 35 for Mg (Klinge 1977). A tendency for Ca, Fe, Mn, and Cu to accumulate in old litter was found, suggesting that they are taken up more slowly than other nutrients (Stark 1971).

Mycorrhizae (composite structures of nonpathogenic soil fungi on tree roots) are thought to be present on most tropical trees and to form hyphae capable of increasing absorption and translocation of nutrients from the soil into the roots (Bakshi 1968). The fungi utilize carbohydrates and probably other growth-promoting substances from the root cells. The mycorrhizal association increases the effective nutrient-absorbing surface and may increase disease and drought resistance as well as the uptake of water and nutrients. Mycorrhizal plants are best suited to exploiting the Oxisols and Ultisols, where P is largely immobilized. Such soils are extensive in the Tropics (Menge 1981).

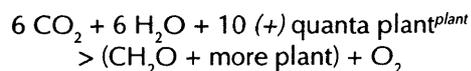
The most common form of mycorrhizae in tropical forests is endotrophic (growing mainly inside the cortical root cells with only a few hyphae outside the root). The more readily visible ectotrophic mycorrhizae form a compact sheath (or mantle) around rootlets, creating a network between cortical cells and the surrounding soil (Mikola 1969). Ectotrophic mycorrhizae are found on the Caesalpinaceae, Dipterocarpaceae, and Pinaceae families and *Eucalyptus* spp. Many mycorrhizal fungi are not highly host specific.

Mycorrhizae are especially common on surface roots in poor soils. In the primary forests on poor sandy soils of Amazonia, most trees are believed to be mycorrhizal (Stark 1971, Went and Stark 1968). Stark (1969) theorizes that when the lakes that once covered much of Amazonia dried up, the forests that developed may have lacked mycorrhizal roots. But then, as soils became poorer through leaching, mycorrhizal species took over.

In summary, it appears that nutrient cycling is the lifeblood of tropical forests. The nutrient supply in established forests is predominantly from recycling rather than from atmospheric fallout or weathering of substrate. Thus, primary forests are largely self-generated, requiring the residual nutrients arising from mortality of organisms for growth and renewal. Any significant interruption of the natural process of nutrient recycling in primary tropical forests will lead to deterioration. To thwart jeopardizing productivity, nutrient levels should be monitored and may have to be replenished.

Tree Growth

Trees grow through photosynthesis, mostly carried on within the leaves. Chemically, the process is expressed as (Bonner 1962):



Of the two known photosynthesis pathways, tropical trees generally use the one designated C_3 . This C_3 photosynthesis is efficient at low light levels but calls for transpiration of about double the quantity of water the C_4 pathway requires, and is sharply constrained by even slight moisture stress (Longman and Jenik 1974). Another critical limitation of the C_3 pathway is its photorespiration, which is greater in the light than in the dark (Chartier and others 1973). Respiration also increases with temperature and at high temperatures (particularly at night) may consume much of the photosynthate.

Living plants respire whether or not there is enough light for photosynthesis. In the dark, they thus consume oxygen (O_2) and produce carbon dioxide (CO_2), whereas, in the light, with photosynthesis offsetting respiration, the opposite is true. Protection from wind may even deter photosynthesis because of a lack of circulation of CO_2 .

Evidence in the Temperate Zone indicates that shade leaves may photosynthesize faster than sun leaves (Helms 1976). On the other hand, the most shaded, oldest foliage can be below the light-compensation point much of the time and, where respiration rates are high, can drain a tree's carbohydrate resources.

Assimilation, also accompanied by respiration, is the storage of photosynthate energy in complex molecular combinations in tree roots, wood, bark, leaves, flowers, and fruits. The apparent assimilation rate is the net consumption of CO_2 . The net assimilation rate is that of the increase in dry matter per unit of leaf area. With an equal leaf area, assimilation will be much less on a poor site than on a good-quality site (Assman 1970).

Growth in dry weight thus requires photosynthetic activity exceeding the respiratory load of the whole plant. Only a small part of the energy stored by photosynthesis benefits tree growth. The respiratory burden may become so great that even an efficiently photosynthesizing plant may not grow (Harper 1977). A balance between photosynthesis and respiration is one of the major features of stable primary forests. As stability approaches, energy is increasingly relegated to maintenance (Odum 1969). Furthermore, as a forest matures, gross production decreases relative to standing biomass, and gross production and respiration approach each other, so that net production is also low (Odum 1969). Thus, changes in

mature forests are mostly qualitative rather than quantitative. For example, in an old montane forest in Puerto Rico, the simple maintenance needs of leaves and roots and soil respiration absorb nearly all available photosynthetic production (Odum 1969). In another instance, Catinot (1974) reports that of 43 t/ha/yr of synthesized dry material examined in Ivory Coast, 95 percent was consumed in respiration, leaving only 5 percent for growth.

Assimilation depends on the nutrients that the plant absorbs. The chief elements determining the geochemistry of the biological cycle of ash constituents and N are silicon (Si), N, and Ca; the second group is K, Mg, Fe, and aluminum (Al); and the third group consists of Mn and S (Bazilevich and Rodin 1966).

Assimilation is accompanied by transpiration of large volumes of water. Production of a gram of organic dry substance may require transpiration of 200 to 1,000 g of water, depending on local conditions (Assman 1970). Assimilation increases with light intensity. Assimilation in the early morning hours may be 10 times as effective per gram of water transpired as later in the day. During normal weather in the Tropics, the rate of assimilation varies during the day, with the highest rate occurring before noon. Rates of assimilation normally drop at midday, apparently because of increased respiration or water stress.

The driving force for transpiration is the gradient in vapor pressure from the leaf to the air when the stomata are open (Whittaker and Woodwell 1971). The evaporating power of the air is determined by its saturation deficit and rate of movement (Schulz 1960). The fall of water potential in the leaf resulting from evaporation losses is the impetus that moves water through the xylem and across all membranes. Evaporation of water through the stomata draws up water and soil nutrients from the roots, thanks to the cohesion of water molecules in the thin vessels of the xylem (Leigh 1975). Transpiration for 20 different tree species in the Venezuelan Amazon was found to range from 2.7 to 1,180 l/d (Jordan and Kline 1977). Evapotranspiration (rainfall less runoff and percolation) measures the simultaneous availability of water and solar energy, the most important rate-limiting resources in photosynthesis. Thus, it has been found to be a highly significant predictor of net annual aboveground productivity of mature terrestrial plant communities (Rosenzweig 1968). Evapotranspiration in lowland rain forests ranges between 120 and 190 cm/yr (Leigh 1975),

about the same as that from an open water surface (Kenworthy 1971).

The potential transpiration rate from dense vegetation that completely shades the ground, is of uniform height, and never short of water is determined by radiation and air movement rather than by species or stand density (Harper 1977). Uneven canopies, particularly in arid regions, produce wind turbulence that may result in a higher transpiration rate than that from a smooth canopy.

Light is fundamental to assimilation efficiency. Fifteen to 25 percent of total solar radiation is lost through reflection and transmission (Rosenberg 1974). Of the remainder, only about 40 percent is in the visible spectrum useful for photosynthesis, between 4,000 and 7,000 nm (angstrom). Of the usable sunlight, regardless of intensity, the chloroplasts of the leaves absorb from 60 to 80 percent (Bonner 1962). However, light saturation of a typical leaf occurs at about 0.1 to 0.2 full sunlight.

A great part of this energy is used to evaporate water (Chartier and others 1973). The basic efficiency of photosynthesis is 105 kcal stored from 520 absorbed, or 20 percent (Bonner 1962). Thus, a leaf that absorbs 80 percent of full sunlight but that can use only 20 percent of that, with a processing efficiency of 20 percent, is operating at an overall efficiency of 5 percent. Under favorable conditions and good management, forest crops thrive on no more than 2 percent of the energy of visible light (Bonner 1962). Such efficiencies are not to be expected generally in nature, although for brief periods in the Temperate Zone growing season, 5 percent has been attained. Common limiting factors are deficiencies in nutrients and water. Under high illumination, CO₂ deficiencies may constrain photosynthesis efficiency by 50 percent, maximum efficiency being near 10 percent of full light (Bonner 1962). Photosynthesis efficiency

depends also on the crown portion that receives enough sunlight for photosynthesis. Overall tree growth may peak in full sunlight, even though photosynthesis of individual leaves may peak well below it (Schulz 1960). Understory leaves tend to have more chlorophyll than canopy leaves (Horn 1971). Four-year growth of a mixture of dipterocarps in natural forests of Sarawak shows the significance of light (table 3-16; Bryan 1981).

Sunlight passing through a forest canopy, particularly when the leaves are in motion, is fragmented into light flecks before reaching the forest floor. In some rain forests and evergreen seasonal forests, these sunflecks make up as much as 50 to 70 percent of the total light reaching the ground (Baur 1964a). Sunfleck light may increase light intensity several hundred times what mean shade density would indicate (Schulz 1960). Furthermore, such light supports vegetation of the lower strata more than its brightness suggests (Evans 1966, cited by Longman and Jenik 1974).

Forest trees differ in "tolerance," which outwardly appears to be the capability to survive and grow under low light intensities. Many canopy trees that live completely exposed at maturity have at their outset withstood years of deep shade until openings occurred that were adequate to stimulate their growth. However, tolerance involves more than shade because suppressed trees, in all but the wettest forests, must also withstand serious water stress induced by larger nearby trees during dry periods. In contrast, seeds of intolerant trees may not even germinate, and if they do, the seedlings may not survive on the shady forest floor.

The allocation of the assimilate within plants has not been well studied. Three-quarters of the photosynthate may be used up in respiration, as seen in a rain forest in Thailand (table 3-17; Kira and Shidei 1967). Of the

Table 3-16.—Light effect on mean annual 4-year d.b.h. growth of dipterocarps in Sarawak (cm/yr)

D.b.h. class	Illumination		
	Full overhead light	Some overhead light	Sidelight only
10-14	0.72	0.44	0.26
30-34	.78	.56	.51
50-54	.95	.53	— ^a

Source: Bryan 1981.

^aNot available.

Table 3-17.—Energy allocation in a Thai rain forest

Parameter	Phytomass (t/ha/yr)	Energy allocation (%)				
		Roots	Stem	Branches	Leaves	Total
Gross production	123.2	6.0	16.5	31.8	68.9	100.0
Respiration	-94.6	-4.5	-10.6	-15.4	-46.3	-76.8
Net production	28.6	.3	2.8	10.4	9.7	23.2
Litterfall	-23.2	— ^a	— ^a	-9.2	-9.6	-18.8
Mortality	-1.2	-.1	-.7	-.2	— ^b	-1.0
Net growth	4.2	.2	2.1	1.0	1.0	3.4

Source: Kira and Shidei 1967.

^aNot applicable.

^bTrace.

remainder, as much as 85 percent may be lost through litterfall and tree mortality, leaving only a small amount for biomass growth. This tally illustrates the low level of assimilate actually allocated to the production of wood. The cost is high, but presumably such production is sustainable.

The allocation of assimilate in trees varies with stimuli such as increased light or growing space. Allocation to the roots, branch terminals, and stem diameter generally takes place in that order (Assman 1970). Growth rings, a reliable indicator of stem growth rates in the Temperate Zone, are not reliable for most species in the Tropics. Most tropical trees do not produce clearly discernible rings, and those produced are generally of unknown periodicity. Growth rings may arise from any of the following anatomical characteristics (Chowdhury 1962):

- Woods that are ring-porous or semiporous (only about 1 percent of tropical trees)
- Less predominant vessels in earlywood than in latewood
- Radially flattened, thick-walled fibers in extreme latewood contrasted with tangentially flattened, thin-walled fibers in the earlywood
- Initial parenchyma cells (found in many families)
- Terminal parenchyma cells (found in one family only).

A study of 60 Amazonian trees disclosed 26 to have no rings at all. Another 22 had clear rings, but these are not

known to be annual (Alvim 1964). Rings may be found in the wood of both deciduous and evergreen trees. There appears to be no relation between the deciduousness of trees and the formation or clarity of growth rings (Chowdhury 1940).

Height growth of tropical trees begins early but diminishes when trees have reached only a third to a half of their maximum stem diameter (Dawkins 1963b). In the Temperate Zone, this is true especially in light-demanding species (Assman 1970). Gap opportunists, such as *Cecropia*, given adequate sunlight, may grow to 10 m in height in 2 years (Schulz 1960).

In primary forests, the topmost trees may be vigorous, or they may have already begun declining in diameter growth, although not necessarily in basal area growth. Canopy trees in middle strata may still be accelerating in growth and may not achieve full vigor until they are much older and larger.

Rapid diameter growth reported for individual trees has suggested a potential for increasing tropical forest production through cultural treatment. An analysis of the diameter growth rates of a mixture of tree species in the rain forests of the Indian Ghats showed that of those 10 cm in d.b.h., some attained 19.5 cm in 10 years (Mathauda 1953). In the rain forests of Nigeria, the most rapidly growing, emergent trees, with a d.b.h. of 101 cm, were estimated to be only 35 years old (Jones 1956). Several dominant species of west Africa, such as *Aucoumea*, *Chlorophora*, *Nauclea*, *Terminalia*, and *Triplochiton*, reportedly are capable of 1 to 2 cm of diameter growth annually for 80 years or more (Catinot 1974). In

what was formerly Zaire, a 7-year record showed that *Macaranga*, *Musanga*, and *Ricinodendron* are capable of more than 2 cm of diameter growth per year (Hombert 1958). Exceptional, exposed trees in the subtropical wet forests of Puerto Rico may grow at the rate of 2.5 cm/yr in diameter (Wadsworth 1958).

However, mean rates of diameter growth in primary forests are far below these extremes. In the rain forests of the Indian Ghats, mean diameter growth rates were reported to be only about 0.3 cm/yr (Mathauda 1953). In Nigerian rain forests, the mean growth rates of even overstory trees of *Khaya grandifoliola*, *Pycnanthus angolensis*, and *T. scleroxylon* were found to be only about 0.7 cm/yr, suggesting that 80 years would be necessary to attain 60 cm in d.b.h. (MacGregor 1934, Webb 1964). For *Azalia africana*, more than 100 years would be required. For trees of 100 cm in d.b.h., the indicated life cycle, based on the mean growth rate, is 135 years (Jones 1956).

In primary subtropical wet forests in Puerto Rico, where both understory and overstory trees were measured, a tree of 10 cm in d.b.h. with average growth was estimated to be 80 years old, whereas one of 50 cm was 260 years (Wadsworth 1958). A summary of the 25-year d.b.h. growth of more than 500 trees in a secondary subtropical moist forest in Puerto Rico gave a mean of 0.12 cm/yr and extremes of 0.04 and 0.58 (Weaver 1979b). Even the dominant and codominant trees were growing only about 0.4 cm/yr. In nearby lower montane rain forests, the corresponding estimates were about 400 and 1,200 years for trees to reach 10 cm and 50 cm in d.b.h. These probably are overestimates, because surviving competitors presumably grow faster than the average.

Jordan (1971b) suggests that tree growth in primary tropical forests is slower than that in the Temperate Zone because of less selective evolutionary pressure toward maximizing efficiency of wood production where solar energy is abundant. Catinot (1974) counters that such comparisons generally use managed forests in the Temperate Zone, to which unmanaged tropical forests cannot be fairly compared.

All such broad generalities about diameter growth, even within species, seem to obscure as much as they reveal. The d.b.h. growth variation within any plot, species, or size class is so wide that means are difficult to interpret. A tenfold difference was found between the slowest and

fastest growth recorded over 24 years for 43 trees of the same species (*Dacryodes excelsa*) and of about the same initial d.b.h. (10 to 20 cm) (Wadsworth and others 1989). Diameter growth rates of *Ceratopetalum* trees in the same plot and of the same d.b.h. class ranged from 1 to 6 mm/yr (Baur 1964a). *Manilkara*, generally considered slow growing in Puerto Rico, may outgrow *Cecropia*, a rapidly growing pioneer, when both are in a closed forest.

Primary forests, by definition, are products of natural (as opposed to human) influences that favor the ecosystem as a whole over the individual organism. One result is that stand density reaches a level that creates intense competition among individual trees, none of which grows unconstrained. Where forest basal area exceeds 32 m²/ha (commonly attained in primary forests), individual tree growth is slow (Dawkins 1959, cited by Ovington 1972). Mean growth is generally derived from a mix of trees growing in different microenvironments, under different degrees of suppression, of different sizes, possibly of different ages, and with different histories of competition. In addition, the growth of some of these trees may reflect effects from causes no longer discernible. So, it is no wonder that individual tree growth in nature varies markedly and generally is far below potential.

The relative importance of different growth constraints is hard to assess. There probably are multiple causes, and those due to competition are difficult to assess. Their effects may persist for decades after the visible evidence of the cause is gone. A tree may also influence its neighbors in many ways other than direct competition for light, moisture, or nutrients. It may produce and release chemical inhibitors (allelopathy); it may shelter pests, carry pathogens, or attract birds or mammals that harm neighboring trees.

One of the most unmistakable constraints on the growth of rain forest trees is shade. The canopy trees absorb 80 to more than 90 percent of the total solar energy (Dawkins 1961b). Maximum assimilation rates and the compensation point between assimilation and respiration are both higher for sun leaves than for shade leaves. Although shade leaves respond more to weak illumination than sun-nurtured leaves, the difference is less than compensating (Chartier and others 1973). Any crown that is higher than neighboring trees has a significantly greater production potential (Assman 1970).

Leaf angles bear out the constraining influence of illumination on the well-being of tropical trees. In the crowns of emergent trees, the leaf angles are more vertical than in the main canopy below (Williams and others 1972). Light saturation occurs at a low intensity; leaves exposed perpendicularly to the Sun's rays may use radiation incompletely. Leaf angles that result in light interception somewhat below saturation can be much more efficient.

Diameter-growth comparisons among tropical trees are complicated by the lack of synchrony in their growth, sometimes even among neighboring trees of the same species (Harper 1977). The time of diameter-growth initiation and the flushing of buds may vary without apparent correlation with external factors (Chowdhury 1940, Longman and Jenik 1974). Eighty percent of the trees in a study of lowland forests in Malaysia were intermittent growers, and nearly all of these were evergreen (Alvim 1964). Only 20 percent were both evergreen and evergrowing. Even among the evergrowing species, growth rates varied during the year. A study of 21 tree species near Belem, Brazil, showed 17 to be clearly periodic in their growth (Moraes 1970). In Nigerian lowland rain forests, five principal timber species were found to grow only seasonally (Amobi 1973). Studies in the wet forests of Puerto Rico showed some species to be more seasonal in diameter growth than others (Murphy 1970).

An early study indicated that cambium cells of deciduous trees do not divide during the leafless period, only after the new leaves unfold. A study of six forest tree species in latitude 30° N. in India (Chowdhury 1939) yielded the following results:

- Diameter growth of the trunk followed foliar development by as much as 2 to 3 months.
- Trees of the same species differed by 1 to 3 weeks in the commencement of growth, unrelated to aspect or spacing.
- Some species had two growth periods.
- No direct correlation could be found between temperature, rainfall, or humidity and commencement and cessation of growth. Hereditary differences were suggested.

In a seasonal climate in western Costa Rica, 12 of 25 upland tree species gained all of their stem growth during the rainy season (Daubenmire 1972).

Growth behavior also varies with the period of the tree's life. Some trees increase their growth rates until they have reached the canopy and their crowns are expanding. After they reach about 60 cm in d.b.h., their growth rate may decline (Jones 1956, Keay 1961, Schulz 1960). Yet in Nigeria, some of the large rain forest trees are capable of increasing their basal-area growth continuously to ages as advanced as 140 years (Webb 1964). Rapid stem-diameter growth through the 30- to 60-cm d.b.h. range has been suggested to explain the paucity of trees of middle sizes in African primary forests (Baur 1964a). Relating diameter growth rate to size is confounded by crown position in the canopy (dominance). These anomalies prompted measurement of tree growth in terms of basal area rather than diameter (Banks 1962, Schulz 1960).

These reports on diameter growth are indicative, but it should be recognized that the use of mean diameter growth is seriously biased. It assumes either that trees are all the same diameter or that their diameters increase throughout life in proportion to their size. Neither is true. Diameter growth is usually much less in large trees than in small ones, yet the wood volume growth in the larger trees may be greater. Use of basal-area growth eliminates much of this bias. Even more bias is eliminated by using basal-area growth as a percentage, which reflects approximately how much a tree grows relative to its root and crown space (as indicated by its stem basal area). Nevertheless, there is still a tendency for this measure to favor small trees over large (Baur 1964a).

Other variations in individual tree growth arise from differences between tree species in the maximum size or age class. The light demanders are initially rapid growers, particularly in the intermediate size range (25 to 60 cm in d.b.h.) (Baur 1964a). But many are short lived, and so the large specimens may not be growing, despite their crown positions.

Past events may well have affected the relative size of two neighboring trees, but they may also be different genetically. Assman (1970) (presumably referring chiefly to the Temperate Zone) attributes much of the variability in tree growth to genetically fixed characteristics, concluding that survival and vigor are linked. Ashton (1969), on the other hand, sees evidence in the lowland dipterocarp forests of selectivity that has produced marked intraspecific genetic uniformity, a seeming paradox considering the numerous species in those forests.

However much genetic differences (genotypes) explain the characters of the different forest trees, each tree is also a phenotype, a result of past events whose effects may be visible indefinitely. An early growth advantage might produce a tree that throughout its life is apparently superior to its neighbors. The end result may be that those trees that are growing more rapidly than their neighbors are doing so partly because their neighbors are not growing rapidly. This could mean that silviculturally removing the slow growers might provide products but would do little to stimulate the trees that are already growing rapidly.

Large tree crowns produce rapid growth in stem diameter. But trees with small crowns are more efficient than those with large crowns in terms of growth per unit of crown surface, crown volume, and area covered (Assman 1970). Vegetable crops behave simply: plants with tall, narrow crowns are more productive per unit of space occupied than plants with short, wide crowns (Jahnke and Lawrence 1965).

Baur (1964b) refers to another variant in tree growth, the "gap opportunists," including species in such important families as the Meliaceae (*Swietenia*) and Dipterocarpaceae. Gap opportunists start on the forest floor but may survive in what appears to be a state of near dormancy for several years, ready to grow upward if light conditions improve.

Relative tolerance explains other growth-rate differences. Schulz (1960) describes the typical canopy species of primary forests as only relatively shade tolerant. These species differ from intolerants only in that they need no light (and may even need darkness) for germination, and they grow more slowly in seedling and sapling stages than typical light demanders. However, at some later stage, more light becomes essential for most (perhaps even all) of the upper and middle story species. During these later stages, light requirements vary widely, but tree growth in all age classes and species is strongly stimulated by added illumination (Schulz 1960).

With these many causes of growth variation, it has been thought unrealistic to assume any relation between the size of trees and their age, other than the vague generality that the largest trees in the canopy are likely to be old. But there is no corollary because the small trees may not be young; they may be as old as the main occupants of the canopy. So it is easy to imagine wrongly that size reflects age.

The entire organic mass arising from the photosynthetic activity of the green leaves of a plant community, including that portion immediately respired, is termed gross primary production (Walters 1973). Gross primary production minus respiration is termed net primary production (table 3-17). Both are expressed in terms of oven-dry organic matter as grams per square meter or as kilograms per hectare (Whittaker 1970).

Poore (1964) points out that there is no evidence that the flora and fauna of primary ecosystems utilize all the habitat's resources. Greater utilization seems possible by using certain plants and animals not naturally available and by concentrating on production from young, rapidly growing individuals. This, however, may not be a sustainable practice.

Ovington (1972) describes the development of a stable forest in terms of productivity. He points out that as forests reach maturity, net primary production diminishes, presumably because of the greater respiration accompanying the buildup of nonphotosynthetic tissue and because of the raising of the forest canopy higher above the soil, the source of water and mineral nutrients for plant growth. He further points out that in mature climax forests, net primary production and loss of organic matter are in balance, the energy captured by photosynthesis being dissipated by respiration. As the climax forest develops, basal-area growth slows. Even though some favored trees may continue to grow, their increment is offset by mortality.

Considering that respiration rates approach the rates of gross primary productivity in primary forests, leaving little for net production, the "increment" in such forests is about the equivalent of mortality and litterfall.

Reproduction

In primary tropical forest ecosystems, trees are not replaced frequently or rapidly. Most of the trees can survive for decades or centuries. Notwithstanding this fact and the many adversities facing seeds and young trees, most tropical forests contain at least a sparse stand of trees well below mature size. One study in a seasonal forest in Venezuelan Guyana showed that 1 in every 10 quadrats of 1 m² averaged 7 trees that were less than 2 m tall (Rollet 1969).

The frequency of heavy flowering and seed years varies widely. Among the dipterocarps, good seed years occur at 1- to 9-year intervals (Cockburn 1975) but may

involve only half the trees. In other years, a fourth of the trees may fruit (Medway 1972). In India, some seeds of most species are available somewhere every year, but not at every location; seed years are variable in periodicity and extent (Griffith 1941a). Overstory species fruit less frequently than understory species. In northern Suriname, most of the canopy species fruit only every second year, including all Vochysiaceae and many Burseraceae, Lecythidaceae, and Leguminosae (Schulz 1960). Long intervals between fruiting may reduce the population of insect predators to a level that permits an oversupply of fruit (and thus more escape to germinate) when fruiting takes place (Janzen 1975). Nevertheless, Harper (1977) points out that not all predators are specialists, so they may move from one species to the next.

In the Temperate Zone, heavy seed years may be accompanied by narrow growth rings, suggesting that abundant seed production slows growth (Assman 1970, Harper 1977). No corresponding observations from the Tropics have been reported.

Tropical plants may belong in any of the following flowering classes (Koriba 1958):

- Everflowering
- Nonseasonal—variation from plant to plant and even from branch to branch
- Seasonal—related to seasonally dry weather or day length (some everflowering and nonseasonal trees of the equatorial Tropics are seasonal in the outer Tropics)
- Gregarious—mass flowering irregularly (some Dipterocarpaceae).

Most of these classes have been found in forests near Manaus, Brazil (Araujo 1970). A 4-year study of 36 timber and latex tree species showed that most flowering occurred in the middle of the dry season (June to November). Flowering may take place once, twice, or several times a year. Some species flower irregularly and are not season dependent.

In the moist forests of Costa Rica, flowering of 42 species peaks in the dry season (Daubenmire 1972). Flowering of periodic overstory trees is heavy in the first 2 months of the dry season (Frankie and others 1974b). Flowering among less seasonal species peaks in May, then tapers

off to November. In the drier forests where rain is normally absent from December to April, about two-thirds of the pollination coincides with the dry season (Daubenmire 1972). In other dry forests of Costa Rica, flowering was greatest in July (107 of 113 species) and decreased until November (Frankie and others 1974b).

In moist lowland forests in Costa Rica, one-fourth to one-half of all tree species have unisexual flowers, and most such species are dioecious, that is, with male and female flowers on separate trees (Bawa and Opler 1975). In a semideciduous forest of Costa Rica, 22 percent of the 130 species were found to be dioecious, 10 percent monoecious, 14 percent self-compatible, and 54 percent self-incompatible (Bawa 1974).

In Malaysia, 26 percent of 722 tree species that grow to 10 cm in d.b.h. or more are dioecious, and these are mostly in the lower strata (Ashton 1969). Among dipterocarps, self-pollination is reportedly usual, although outcrossing takes place within clumps. Primary forest conditions are believed to select against outcrossing and intraspecific variation (Ashton 1969, Fontaine 1976). Because a tree's survival in a dense forest probably depends more on the hazards of its surroundings than on genetic suitability, adaptation does not vary greatly among individuals.

Much remains to be learned about the role of insects in pollinating rain forest trees (van Steenis 1972); floral fragrance does not fully explain this role. There is much variation among species, even within genera.

Published information is generally sparse on the length of time between flowering and ripening of fruit of many potentially important tropical trees for which seed collection can be anticipated. Systematic documentation of such information has reportedly begun in Malaysia (Ng and Loh 1974).

Within the year, there are single peak periods of seeding, even in rainy climates (Medway 1972). Certain gap opportunists and understory species may bear mature fruits much of the year (Baur 1964a). But most fruiting is clearly seasonal, although the actual dates may shift from year to year (Baur 1964a, Harper 1977).

The amount of fruiting fluctuates in seasonal climates. In Colombia, fruiting was less equitably distributed throughout the year in seasonal environments than in premon-tane wet forests (Hilty 1980). In Costa Rica, fruiting peaks

at the beginning of the wet season and then again after the July-to-August “veranillo” (dry spell) in September and October (Fournier 1976b). Nevertheless, some species may be in fruit at any time (Daubenmire 1972, Frankie and others 1974b). In Puerto Rico, seeds of introduced *Swietenia* mostly fall near the beginning of the dry season, but seeds of most other species fall during the wet season.

Seed dispersal in closed tropical forests—like pollination—does not generally depend on the wind. Minimal air movement makes wind pollination unreliable within deep forests (Baur 1964a). Near Manaus, Brazil, pollen of only 5 of 37 tree species was found to be wind disseminated (Silva 1977). Seeds with wings are the only type that can “fly” over a long distance in the still air common to many tropical forests (Harper 1977).

Wind dispersal of seeds in Suriname is limited largely to upper story trees and the pioneer species (Schulz 1960). In a study in Nigeria, 46 percent of the overstory species proved to be wind dispersed, compared with only 8 to 9 percent of the lower story trees (Jones 1956). In a seasonal wet evergreen forest of Venezuela, more than 20 percent of the trees measuring 60 or more cm in d.b.h. produced wind-disseminated seeds, compared with only 5 percent in the understory (Rollet 1969). In Panama, the April fruiting peak consisted mostly of wind-dispersed seeds; the August fruiting peak did not (Croft 1975).

Animals are the most common means of seed dissemination in tropical forests (Baur 1964a, Janzen 1975, Schulz 1960). In fact, seed dissemination is believed to be the most important contribution of tropical mammals to forest ecosystems of the region (Fleming 1975). Wherever new growth shows little species correlation with nearby seed trees, animals are considered responsible for seed dissemination (Baur 1964a). Some linkage to animal behavior is generally observed when seeds have not been wind dispersed (Harper 1977, Jones 1956). Along large rivers, seeds may be disseminated even by fruit-eating fish (Prance 1982). In Nigerian rain forests, fruits edible by animals were found on 46 percent of upper story tree species and on 70 percent of those in the middle and lower stories (Jones 1956).

Seeds of almost all understory species of the montane wet forests of Colombia are distributed by birds (Hilty 1980). Near Manaus, Brazil, seeds of 22 of the 37 tree

species studied, or 60 percent, were disseminated by birds (Silva 1977). The fruiting seasons of different species of *Miconia* are so staggered that fruits of some species are available in all seasons.

Snow (1981) lists the following genera in the diets of frugivorous (fruit-eating) birds. Those designated “(s)” are fed upon by specially adapted species: *Alchornea*, *Allophylus*, *Aniba* (s), *Ardisia*, *Bactris* (s), *Beilschmeidia* (s), *Bromelia*, *Bursera*, *Byrsonima* (s), *Canella*, *Capparis*, *Casearia*, *Cecropia*, *Chlorophora*, *Chrysophyllum* (s), *Citharexylum*, *Clusia*, *Coccoloba*, *Comocladia*, *Cordia*, *Cupania*, *Dacryodes*, *Dendropanax*, *Eugenia*, *Fagara*, *Ficus*, *Genipa*, *Guaiaecum*, *Guarea*, *Guazuma*, *Hedyosmum*, *Henrietella*, *Heterotrichum*, *Hieronyma*, *Hirtella* (s), *Ilex*, *Lactea*, *Licaria*, *Manilkara*, *Margaritaria*, *Matayba*, *Metopium*, *Miconia*, *Myrcia*, *Myrica*, *Nectandra*, *Ocotea*, *Palicourea*, *Persea*, *Petitea*, *Picramnia*, *Piper*, *Pisonia*, *Pithecellobium*, *Pouteria*, *Prestoea*, *Psidium* (s), *Psychotria*, *Rollinia*, *Rourea*, *Roystonea*, *Sapium*, *Schefflera*, *Sloanea*, *Tetragastris*, *Trema*, *Trichilia*, *Trophis*, *Turpinia*, *Virola*, and *Zanthoxylum*.

Despite the prevalence of animal dispersal, extremely concentrated distribution of seedlings of most species near parent trees has been observed (Jones 1956, Schulz 1960). In Suriname, this apparently caused the patchy distribution of many of the canopy species. Contiguous distribution of trees in Malaysian dipterocarp forests also has been ascribed to inefficient seed dispersal (Ashton 1969, Burgess 1975). Natural regeneration of dipterocarps is usually within 60 m of seed trees.

Once seeds reach the forest floor, most can germinate early under favorable conditions. A test of the seeds of 99 tree species in Malaysia showed that 70 percent of the species germinated clearly within 12 weeks, 7 percent had begun clearly after the 12th week, and the rest either before or after 12 weeks (Ng 1973).

In the forests of northern Suriname, early germination is critical to success for most of the tree species of the middle and upper stories, because seedlings must be waiting when a canopy opening favors them (Schulz 1960). Moreover, evidence from both hemispheres indicates that the seeds of many tree species are perishable (Gomez-Pompa and Vazquez-Yanes 1972, Webb and others 1972). Even those that are not may be attacked by insects or microorganisms within a few days or weeks (Schulz 1960).

Light-demanding pioneer species and some gap opportunists may require light for germination and, therefore, may need to persist on the forest floor before germination (Schulz 1960). Gap opportunists capable of germinating in the shade may still have to withstand dry weather. Some need to be in direct contact with the mineral soil to germinate (Schulz 1960). The fresh seeds of *Schefflera morototoni*, a forest pioneer, sown in nurseries in Puerto Rico, did not germinate for many months, indicating physiological dormancy (Wadsworth 1945). Four sources of such apparent dormancy have been recognized (Harper 1977): (1) seed development incomplete until after dispersal; (2) need for germination to be triggered by photoperiod, light, or temperature; (3) need to overcome an inhibitor in the seedcoat, and (4) water access restricted, usually by an impermeable seedcoat.

Species with seeds that lie dormant before germination need defenses against predation. Some carry toxic compounds. Thick seedcoats and pericarps may also provide protection. Small seeds may be safer than large seeds. Seeds bearing awns or spines tend to escape predation. Brief dormancy also favors protection against predation (Hunter and others 1977). Species adapted to poor environments, where competition may be intense, tend to have larger seeds and devote more of the limited resources to survival of established individuals than to fecundity (Harper 1977).

Variations in proximity to seed trees, size and recency of seed crops, and seed durability all affect the abundance of tree seeds on the forest floor. Studies near Veracruz, Mexico, showed the presence of many dormant seeds on the forest floor (Guevara Sada and Gomez-Pompa 1976). Collections in both Mexico and Nigeria showed seeds of upperstory species to be rare and never present throughout the year (Gomez-Pompa and Vazques-Yanes 1972, Keay 1960). Seeds of secondary species, in contrast, were abundant continuously, suggesting either greater durability on the soil or more frequent seed production. In the dipterocarp forests of Sabah, only 38 percent of the seeds collected in one study were of primary species (Liew 1973a). The seeds of pioneers such as *Anthocephalus* and *Macaranga* were abundant. These relationships sound logical, but the real differences in seedling abundance are governed also by the capacity of the seeds to germinate.

Much tropical forest regeneration takes place where the canopy has been broken (fig. 3-4). The following three

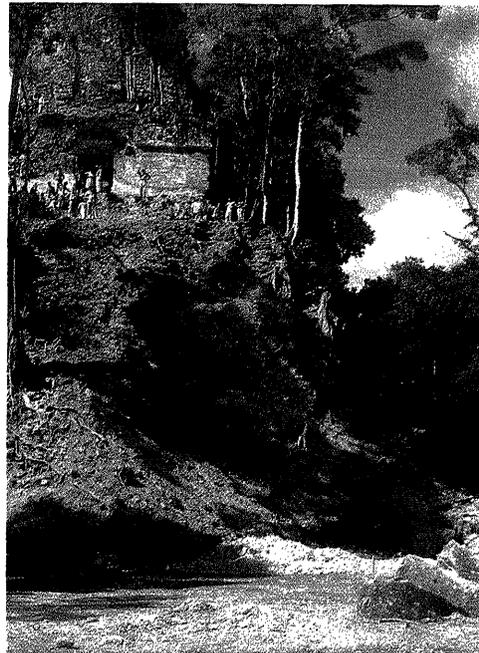


Figure 3-4.—The regenerative power of tropical forests is seen in the trees that totally cover and hide from view the great pyramids of the Mayan city of Tikal.

degrees of disturbance and their respective regenerative responses have been distinguished (Baur 1964b):

1. The death of a single, medium-sized tree may create an opening smaller in diameter than the canopy height, one that will be closed rapidly by adjacent tree crowns, prompting a surge in gap opportunist species that will soon disappear.
2. When a large tree falls, creating a canopy gap of at least 1,000 m², the opening stimulates regeneration of secondary species that may survive and reach maturity, enduring for many decades and contributing to a common species "patchwork." An example of such a secondary species in tropical American forests is *Cordia alliodora*, the seedlings of which may survive suppression up to 8 months, yet require a gap to develop (Tschinkel 1965).
3. Where a catastrophe "flattens" a larger area of forest, gap opportunists will leap ahead and fill the gap with light shade, beneath which longer lived species can develop at a slower pace and later succeed them.

In mixed tropical forests, the death of a tree apparently seldom favors replacement by the same species, despite a tendency for seed accumulation there. Long ago, a theory was developed in west Africa that the environment created beneath one primary forest tree species favors the progeny of others more than its own (Aubreville 1948). This theory was designated "mosaic" by Richards (1952). Although Schulz (1960) reported no evidence to support this theory in the rain forests of northern Suriname, it does seem that some mechanisms must favor a sequence of changing species. Evidence that seed predation is greatest near the parent tree supports the concept (Janzen 1970b). It has been reported that for this reason progeny of *Manilkara bidentata* do not grow up beneath their parents (Baur 1964a, 1964b).

There is also evidence to support such a theory of sequential change in species in Temperate Zone forests. There, the tendency for tree replacement by different species is due to much more than mere selectivity by insect predators (Fox 1977). Seed or seedling survival may be controlled by other predators, parasites, toxins, and direct competitors instead of insects.

Plant behavior after seed germination is critical to success in the competitive environment of primary forests. Two routes to success, as follows, have been recognized by Harper (1977):

1. Light demanders result from an evolutionary, selective force toward many descendants and precocity. Selection favors allocation of much of the assimilate to seed production. Neither competitive capability nor length of life is favored. Progeny that are produced late in life are unimportant because succession has progressed too far for them to become well established.
2. Plants that come up in an already established forest are classed as tolerant and are more aggressive than fecund or precocious. They produce larger but fewer seeds, survival during a juvenile period and longer life becoming more important than seed production. When two such species are grown together, selection favors divergence so that competitive demands on the mutually required resources are minimized.

The number of progeny per species in the forest is not proportional to the number of mature trees (Harper 1977). Apparently the reproductive capacity of a forest tree does not alone determine its abundance. Important also is the capacity of the progeny to survive hazards

during the period of early growth and development. As an example, the survival of dipterocarp seedlings in a study in north Borneo decreased from about 80 percent after 1 year to 43 percent after 5 years (Nicholson 1965b). In Puerto Rico, seedlings of the opportunist *Tabebuia heterophylla* may cover the floor within moist forests from early in the rainy season until the next dry season, when they nearly all disappear.

The complex factors involved in the natural regeneration of primary tropical forests are not well understood. Past interest in exploiting these forests for timber has concentrated on a few merchantable overstory species. The adequacy of natural regeneration was assessed in terms of the sapling density of only those species. Except for dipterocarp forests on the best sites (Tang and Wadley 1976a) and a few other special circumstances, advance regeneration of these species was inadequate for a second crop composed entirely of such species. This conclusion, notwithstanding the gradual, continuous process of natural regeneration that in nature maintains primary systems, results from the limited number of species that have been acceptable on the market and unwillingness to accept the natural timespan for this process.

Where natural regeneration of a few selected timber species has been considered inadequate, it has been assumed that a thinned overstory and a prepared seedbed beneath it would engender a good crop of these species within a few years. This assumption, too, seems to have been at odds with the capability of these timber species as seedbearers or as competitors in a liberated understory. This subject is discussed more fully in the next chapter.

Environmental Influences

Responses of primary tropical forests to their environment plus the reciprocal influences of forests on the environment are considered here from the standpoint of productivity. Many of the biological variations in tropical forests are merely different points along continua rather than abrupt changes. These variations usually result from more than one cause, and these causes do not all affect the forests at the same rate or in the same way. Therefore, differences may appear gradually, and it is difficult to describe them discretely or to ascribe them to specific causes. A complicating factor is doubt as to how precisely apparently undisturbed forests represent natural conditions of the present or recent past. Sauer (1957) makes a case for questioning this point almost everywhere that drainage and relief are favorable for former

human habitation. It has been said that there may not be a single climax forest in all of Africa. Findings throughout the Amazon Basin bear witness to former habitation, at least on certain soil types, and some of these sites are not even accessible. The restoration of a primary rain forest, despite rapid early filling of gaps, presumably takes more than a generation of the climax species to reach stable composition. Thus, what appear to be primary forests, however seemingly undisturbed by human intervention, may indeed have been influenced by early human activity.

Geographical isolation greatly affects forest productivity, especially on oceanic islands (MacArthur and Wilson 1967). Small islands may have fewer habitats than would an equal area on a continent because of less immigration and differentiation in dispersal mechanisms. The number of species on a given island is usually related to the island's size, as is environmental diversity, which more directly relates to species numbers.

Catastrophic weather phenomena (e.g., hurricanes) have unmistakable and lasting effects on the character and development of forests. Where hurricanes pass frequently, forests may resist winds well but lack internal stability, retaining a higher proportion of seral (successional) characteristics than elsewhere. Hurricane-lashed forests generally suffer tree-crown breakage and unidirectional uprooting. Surviving trees tend to produce buttressed roots, short stems, dense wood, and compact crowns of coriaceous leaves (King 1945). The fact that they have survived hurricanes does not mean that they do not suffer damage or take a long time to recover. The trees may resprout and replace crowns even at advanced ages, but the effects of breakage may never entirely disappear. For a recent report on the influence of hurricanes on tropical forests, see Walker and others (1991).

Environmental relationships of forest ecosystems are two-way. The forest has a general ameliorating effect on environmental extremes. Within primary forests, the microclimate varies from the top of the uppermost tree canopy, where exposure to the elements may be similar to that in deforested areas, to ground level, where external effects are moderated, producing a relatively equable environment (Baur 1964a). At the ground level, stability of litter, soil, water, and nutrients promotes sustainable forest productivity.

Moisture. Moisture is the most important environmental factor determining distribution, species composition,

and growth of forests (Kozlowski 1982). Forest productivity is closely correlated with moisture availability. From wet to dry environments, forest height declines from 50 to 10 m or less. Of significance to wood production is the great difference in the amount of stemwood under different moisture conditions. Veillon and others (1977) found stemwood in Venezuelan forests to range from 35 percent where mean annual rainfall was 40 cm to 65 percent with 260 cm of rainfall.

Available moisture is also significant to other structural features. Evergreen seasonal forests and rain forests in Cambodia and Thailand with similar biomass had leaf area indexes of 7.3 and 10.7 to 12.3, respectively (Art and Marks 1971). There is less layering of vegetation in dry forests than in wet forests, and many of the special life forms are absent (Webb 1959).

Seasonal climates characteristic of the outer Tropics are very significant to forest growth. Schulz (1960) concluded that drought in Suriname is chiefly responsible for periodicity of growth. As already mentioned, stems grow mostly in the wet season.

Primary forests first encounter rainfall as it is intercepted by tree crowns. Data on the average amount of rainwater intercepted are meaningless because the degree of canopy cover and the intensity and duration of the rainfall vary widely. A study in the rain forests of Panama showed that interception percentage increased with canopy cover and was greater during light showers (Golley and others 1975). A similar relation was found in the moist forests of Puerto Rico (Clegg 1963). With a rainfall of 0.13 cm, interception was complete; with a rainfall of 2.03 cm, only about 50 percent was intercepted.

In Thailand, interception varied markedly with the forest type, being greater in the dry forests (Chunkao and others 1971). On days with rainfall between 0 and 1 cm, mean interception in evergreen forests was 24 percent, compared to 78 percent in dry dipterocarp forests. For days with from 2 to 3 cm of rainfall, the corresponding percentages were 14 and 64. Also, interception declined with increasing rainfall as the canopy reached saturation. The higher interception rates for the drier forests are not clearly explained, but may well be due to less intense rainfall in these areas even when the day's rainfall is substantial.

Intercepted water is less than a total loss to the ecosystem because it joins the system as water released through

the stomata, absorbing heat in the process of evaporation and contributing to atmospheric humidity nearby (Monteith 1975). There is no significant humidity gradient at night, the atmosphere at all levels being near saturation (Davis and Richards 1933/34). Relative humidity in a terra firme forest near Belem, Brazil, measured for a year (Bastos and others 1974), showed year-round constancy of air saturation at night, even 15 m above the ground (table 3-18; Bastos and others 1974). Even at noon, no real humidity stress is evident. Evaporation and transpiration prevent the air from drying out. In Nigerian rain forests, little or no water vapor was lost from the lower to upper layers during the day (Evans 1966).

Dew at night could compensate, in part, for interception. As the temperature drops, the atmosphere is generally at or near the saturation point. Nevertheless, in some Nigerian rain forests, no dew falls to the ground (Evans 1966). Another study found that dew is retained by small leaves; only the large digitate leaves of *Musanga* accumulate sufficient dew so that some of it drops (Longman and Jenik 1974).

Of the water that passes through the foliage, the fraction that flows down the stems of the trees is insignificant except during the most intense storms, according to one study in Malaysian rain forests (Kenworthy 1971). About 1 percent of the water received evaporated from the soil surface, and only 3 percent ran off the soil surface, indicating that 96 percent percolated into the forest soil. The basal streamflow, including surface runoff, totalled about 25 percent of the rainfall. Base flow was reduced during the day because of more active transpiration, estimated at 135 cm/yr.

Temperature. As would be expected, temperature (especially minimum temperature) affects plant growth in the Tropics. For example, the minimum temperature of the outer Tropics is lower than that of the equatorial Tropics, adversely affecting the flora.

Vegetation on tropical mountains may also be affected by low temperature, but the effect is confounded by differences in rainfall, wind, and cloudiness. Nevertheless, Grubb (1977) found that as elevation increases in wet tropical forests, height drops from 42 to 2 m and species richness, leaf size, buttresses, and climbers decline. He concludes that the upper elevational limit of species occurrence is probably determined by temperature, whereas the lower extreme is probably determined by competition. He also sees nutrient deficiencies changing with elevation and transpiration reduced by cloudiness. At high elevations (and low temperatures), the trees became crooked as on poor, lowland soils. Moreover, at low temperatures, large amounts of available N and P are locked up in undecayed litter and unmineralized humus.

The effect of elevation on plant growth is not consistent, however. A study in Venezuela (Veillon 1965) indicated that the number of trees, basal area, and volume in primary forests do not decline with elevations up to 3,000 m. A similar conclusion was reached comparing tropical (>24 °C) and premontane (12 to 18 °C) vegetation in Panama (Golley and others 1969).

Plant growth rates are affected by both day and night temperatures as well as by day length (Longman and Jenik 1974). Photosynthesis is believed to be most

Table 3-18.—Mean relative humidity in a terra firme forest near Belem, Brazil, by month, time of day, and height above ground (%)

Month	Relative humidity			
	1.5 m above ground		15 m above ground	
	Noon	Midnight	Noon	Midnight
January	91	99	80	99
April	92	100	84	100
July	71	94	66	99
October	78	95	66	97

Source: Bastos and others (1974).

efficient and plant growth most rapid at about 30 °C (Thornthwaite 1948). Chang (1968, cited by Scott 1976) believes that because respiration as well as photosynthesis varies with temperature, net primary production of ecosystems is relatively unaffected by moderate changes in mean temperature.

The forest's buffering effect may reduce the daily temperature range to less than a third of that outside the forest (Baur 1964a). In a Nigerian rain forest, heat input into the lower forest strata from 10 a.m. to 7 p.m. averaged 10 kcal/m²/h, and heat lost at night averaged 7 kcal/m²/h (Evans 1966). No heat was lost from either upper or lower layers during the day, heat transfer occurring mainly at night.

Temperature variation within a terra firme forest along the Amazon, near Belem, was minimal during both the day and the year (table 3–19). However, the temperature at 15 m above surface level is higher than that at 1.5 m at noon and lower at midnight (Bastos and Diniz 1974).

Bastos and Diniz (1974) found greater uniformity in soil temperatures beneath the forest than in open areas; they also found that the difference in temperature between forest and open land is greater at the surface than 1 m below (table 3–20).

Brinkman and Goes Ribeiro (1971) found that at 2 cm above the ground surface under the primary forest in central Amazonia, the temperature rose above 30 °C only 3 percent of the time, and the maximum reached was 33.9 °C. In the open, they found the corresponding temperature was above 30 °C 52 percent of the time and reached a maximum of 49.9 °C.

Light. Light reduction within forests is gradual from the tree canopy to ground level. Yoda (1974) found that visible illumination received at 57 m above ground in a Malaysian rain forest drops to 30 percent at a height of 40 m, 20 percent at 30 m, 5 percent at 20 m, 2 percent at 10 m, and 0.5 percent at 1 m. In a Suriname rain forest, 1.5 percent of full sunlight prevailed in the undergrowth (Schulz 1960). The level found in a terra firme forest near Manaus, Brazil, was 1.4 percent (Conceicao and Barros 1979). Another study showed a maximum at noon of 0.1 percent, declining to 0.05 percent by 3 p.m. and to 0.02 percent at 4 p.m. (Longman and Jenik 1974). Of the 2 to 3 percent reported for Malaysian and Nigerian rain forests, from 5 to 6 percent is direct skylight, 25 to 44 percent is transmitted light, and 50 to 70 percent is sunflecks (Baur 1964a).

Because of the distance between the canopy and the soil, most gaps in the canopy are smaller than the Sun's apparent diameter, and thus a large amount of the transmitted light is in penumbra zones, resulting in relative uniformity of illumination at the forest floor (Chartier and others 1973).

The decreasing light with depth beneath a forest canopy results in tree suppression. In a Puerto Rican forest with 1,566 trees of 5 cm in d.b.h. or more per hectare, only 4 percent were dominant; 10 percent were codominant, 32 percent intermediate, and 54 percent suppressed (Anon. 1953a). The relative d.b.h. growth rates of these four classes indicate, in part, the significance of illumination. If the mean diameter growth rate of dominant trees is set at 100, the codominants may grow at a relative rate of 90 to 110, the intermediates at about 50 to 70, and the many suppressed trees at only 10 to 30. Under these

Table 3–19.—Mean temperature variation in a terra firme forest in Brazil by month, time of day, and height above ground (°C)

Month	Noon		Midnight	
	1.5 m above ground	15 m above ground	1.5 m above ground	15 m above ground
January	26.7	27.6	23.6	23.1
April	27.1	28.7	24.6	24.8
July	27.5	28.1	23.6	23.0
October	27.7	28.6	23.4	23.0

Source: Bastos and others 1974.

Table 3–20.—Soil temperatures near Belem, Brazil, by month, depth, and type of land (°C)

Month	2-cm depth		1-m depth	
	Forested	Open	Forested	Open
January	25.2	31.3	25.1	28.4
April	25.3	31.6	24.9	28.6
July	25.4	36.8	25.0	29.2
October	25.1	40.2	25.0	30.0
Average	25.2	35.1	25.0	29.1

Source: Bastos and Diniz 1974.

conditions, a tree of 30-cm d.b.h., which has spent much of its life suppressed and still may be only an intermediate, may be 180 or more years old.

Soils. Tropical forests have evolved toward maximum use of available soil nutrients. In rain forests, the limiting nature of nutrients vis-a-vis moisture and temperature highlights mechanisms of adaptation to nutrient deficiencies. On the most infertile soils (e.g., Podsolis and peat swamps), rain forests include those species with a tolerance for such deficiencies, although they may be able to meet the keener competition among trees characteristic of more favorable sites.

On nutrient-poor substrates, such as Latosols near Manaus, Brazil, the nutrient content of fine roots is generally lower than elsewhere (Klinge 1976). Adaptations to these conditions include (Herrera and others 1978): (1) dense root mats with high nutrient retention capacity; (2) direct nutrient cycling through mycorrhizae; (3) accumulation of chemicals in the leaves (herbivory reduction); (4) recovery of nutrients by leaf shedding; (5) resistance to Ca deficiency, Al abundance, and acidity; (6) litter arrangement on the forest floor so as to reduce leaching; and (7) epiphytic fixation of N from the air.

Serpentine soils may be especially inhibiting to growth because of unfavorable physical factors such as high Mg, nickel (Ni), and possibly chromium (Cr) levels, or low Ca or nutrient levels (Proctor and Woodell 1975). Tree adaptations may include favoring uptake of some elements and not others or tolerance of high levels of Mn, Cr, cobalt (Co), and Fe. The effect is to exclude all but the most tolerant or adaptable species.

Poor soils reduce forest stature as well as richness of composition. The cerrados of Brazil, forests characteristic

of poor soils, grow to only 12 m in height and no more than 70 cm in d.b.h. (Rizzini 1975). Schulz (1960) described an exception in the savanna forests of the white sands of Suriname. He reported that small areas of white sand may be wholly covered with tall rain forests, apparently because roots extend down 5 m to the decomposing rock.

Conversely, favorable soil conditions are reflected in the quality of primary forests. The abundance of natural regeneration of sal (*Shorea*) in India increases with the availability of N and P in the soil (Seth and Bhatnagar 1960).

Mangroves manifest the significance of adverse soils to natural forests (fig. 3–5). Flooding and the presence of salt favor the mangrove species because it is the only



Figure 3–5.—Mangroves produce dense cover over the shores of estuaries and tidal swamps.

species that can tolerate these conditions. Segregation of species within the mangrove may also be sharply defined. In Sabah, the occurrence of two species of *Rhizophora* is clearly related to distance from the seafloor. *Rhizophora apiculata* is most abundant about 250 m from the front, whereas *R. mucronata* is at its maximum abundance 650 m from the front (Liew and others 1975). *Avicennia* is favored where salinity becomes higher than the other species can tolerate.

Experiments in Hawaii with common tropical soils—Oxisols, Ultisols, Inceptisols, and Histosols—show the influence of forests on soil porosity (Wood 1977). Infiltration rates under forests were three to five times as great as in comparable soils under pasture, sugarcane, and pineapples. Infiltration rates in the forest (measured with concentric ring tests) ranged from 15 to 39 cm/h whereas the highest rates for pasture were 5 cm/h, for sugarcane, 3 cm/h, and for pineapples, 9 cm/h. The larger soil aggregates under the forest also lower susceptibility to erosion.

Topography. Major differences in primary tropical forests as a result of elevation have already been pointed out. Less well known is the influence of local topography within different forest types. Ridgetops in wet climates are better drained than valley bottoms and may have more newly weathered material available, but they are also more erosion prone. In contrast, valley bottoms in dry climates have more available moisture and benefit from colluvial deposition.

Studies of mountain forests in Puerto Rico showed long ago that there was segregation of tree species on the basis of local topography (Wadsworth 1953). Even though hills and valleys may be very close, mature trees of some species occur chiefly on one and only occasionally on the other. *Dacryodes excelsa*, for example, is usually found near the ridgetops, whereas *Guarea guidonia* is usually on lower slopes or valley bottoms.

Stand density is also influenced by topography. In the dipterocarp forests of Malaysia, the total number of trees per hectare larger than 27 cm in d.b.h. was 58 on the ridges versus 33 in the valley bottoms (Wyatt-Smith 1960c). For the economic species, the corresponding numbers were 30 and 11. The disparity among large trees is more extreme. In the same area, Burgess (1970) later classified the lower hillsides as marginal for timber production and excluded the valley bottoms and slopes in excess of 45°.

Topography, and more specifically aspect, may be significant to forest productivity in much of the Tropics where there is a pronounced prevailing wind direction. In the tradewind zone of the outer Tropics, eastern slopes may present a surface perpendicular to the slanting fall of wind-driven raindrops, whereas western slopes may be nearly parallel. The effect may be greater rainfall and erosion on eastern slopes, leaving shallow soils that cannot absorb and retain much rainwater. Evaporation, also a result of the same prevailing wind, may then leave exposed slopes drier than protected ones.

Growth-Prediction Experience. Attempts to correlate the diameter growth of individual trees with competition and tree size have not been very successful. In Puerto Rico, no correlation was found between the diameter growth of *Dacryodes excelsa* and the basal area of neighboring trees within 8 m, although initial diameter and crown class did explain about a third of the variability (Wadsworth 1953). In northern Nigeria, girth, height, and crown size accounted for 40 percent of the variation in subsequent growth (Kemp and Lowe 1970). Density, expressed by relascope count, basal area of competitors, and summed height of competitors, accounted for 19 percent more. Site variables accounted for an additional 14 percent. In another area of Nigeria, about 70 percent of the variation in diameter growth among the trees was related to their own basal area (Lowe 1971). Height and crown diameters were strongly correlated with basal area but did not account for additional variation in growth. Competition did not account for more than 5 percent of the variation in growth, even where competition was evidently strong. Drainage and topography did not account for a significant portion of the variation in growth.

A 24-year study of 1,560 trees in subtropical wet forests in Puerto Rico showed a marked decline in percentage basal-area growth above 35 cm d.b.h., more rapid growth on valley bottoms than on ridges and on steep versus flat slopes, and 70 percent more growth on dominant trees than suppressed ones. Such studies clearly are dealing with complex multivariate relations still little understood. One hypothesis is that in stable forests the proximity of trees so reflects soil quality that individual tree growth is about the same regardless of surrounding forest density.

Other Effects. Wind speeds are sharply reduced within tropical forests. A study of wind velocities in a wet forest in Colombia during January to April showed that if wind

velocity at 60 m above the ground surface is rated 100, the corresponding rate in the treetops at 42 to 45 m is 30 (Baynton 1965). At half the canopy height, the rate is 3, and at 2 m above the ground, the rate is 1, suggesting that wind and light are reduced by about the same magnitude.

A dense tree barrier may protect a downwind area 10 to 15 times the canopy height (Rosenberg 1974). Paradoxically, forests that are open near the ground allow wind through that slows the downwind descent of the turbulent air that has been forced upward by the canopy, increasing significantly the length of the downwind reduction in mean velocity at the surface.

The fact that forests reduce soil erosion is well known. The significance of this attribute increases with steepness of slope and intensity of rainfall. Mangroves in estuaries significantly trap sediment arising in tropical watersheds. The mangrove initially follows sedimentation, but once established, mangrove stilt roots slow and precipitate additional sediments (Watson 1928).

Soil degradation in humid climates is inevitable in level areas unless there is an outside nutrient source (Assman 1970). On slopes, weathering of parent rock may continuously replenish nutrients. This process is partially responsible for the lasting productivity of forests on slopes. Additional nutrients may be made available by chelation. Many forest plants appear to produce chelating agents that expedite soil formation (Longman and Jenik 1974). Even so, in ferralitic (iron-containing) soils, few undecomposed, nutrient-rich minerals are generally left within reach of plant roots. The cation-exchange capacity of these soils is very low except for the thin layer of humus at the top, a direct product of the forest itself.

Yields

The yields of primary forests may be expressed in different ways, based on their increment rate and depending on the evaluation criteria applied. Ecologists see yield in terms of net primary production, which is gross primary production minus respiration. This is equal to net growth of all organisms, above and below ground, plus the litter produced. Then, because the traditional forest products utilized are mostly made from tree stems or from stems and branchwood, the volume increments of these forest components are of special interest to the timber producer. Finally, there is the yield expressed in terms of merchantability. This excludes stemwood that is not

economical to harvest, because of species, small size, crook, or defects and, generally, bark and, possibly, sapwood, slab, edgings, and sawdust, depending on the product.

Primary Productivity. Gross primary productivity of primary closed tropical forests ranges between 13 and 123 t/ha/yr (Golley and Lieth 1972). It is estimated that 60 percent of the total primary productivity of the Earth's land surface is in the Tropics, and another 20 percent is in the sub-Tropics (Rodin and others 1975). Subtracting respiration, net primary productivity ranges from 10 to 32 t/ha/yr (Murphy 1977) and is related to temperature and precipitation (table 3-21) (Lieth 1972). It also varies by forest type (Rodin and others 1975):

Forest type	Net primary productivity (t/ha/yr)
Tropical	
Humid	27-30
Seasonally humid	15-16
Flood plains	70
Mangrove	10
Semiarid	7-14
Subtropical	
Humid	16-22
Montane	18
Semiarid	5-10

Primary productivity of a tree community is related to the growth of the usable stemwood to a 7.5-cm limit (Dawkins 1961d). Annual turnover (leaves, nonpersistent twigs, inflorescences, and fruits) generally ranges between 20 and 30 percent of a tree's dry weight wood accretion. Dawkins concluded that it is highly unlikely

Table 3-21.—Relationship of climate and net primary productivity

Mean temperature (°C)	Mean annual precipitation (cm)	Net primary productivity (t/ha/yr)
10	100	14
20	200	22
30	300	26
30	400	28

Source: Lieth 1972.

that the total primary production of a tree community would exceed 1.6 times the easily measured stemwood growth.

Useful Wood. Except where fuelwood is important, stemwood productivity is the best measure of prospective useful wood yield. Stemwood makes up 70 to 80 percent of the aboveground phytomass of primary forests (Dawkins 1961d). Dawkins (1964b) studied tree diameter growth relative to relascope basal area, crown exposure, and lateral interference. He concluded that, with 90-percent crown cover and the greatest practical crown freedom, maximum wood yield is about 11 t/ha/yr. Weck (1963), cited by Bazilevich and Rodin (1966), came to a similar conclusion.

In commercial forests, the merchantable yield is not the same as net primary productivity. Not only are the roots of no direct concern, but neither are the termini of the stems, the leaves, or (usually) the smaller branches. Furthermore, maximum economic return may not relate directly to maximum volume production because, for most products, large trees are generally worth more than an equal volume in small trees.

Quantity of useful wood per unit of forest area (which may be independent of quality) is of paramount concern. As Gallant (1959) pointed out many years ago, the tropical timbers most in demand in world trade are among those most common in the forests. While any species that grows to useful dimensions and is of good form is likely to be accepted in expanding local markets, those woods that can be obtained in quantity will still be preferred.

Hughes (1968b) observes that it would be unwise to assume that changing use patterns and improved technology will eventually solve the problems of utilizing all species now considered secondary in quality. There are usually good reasons for classifying a species as secondary. It is unlikely that such problems as difficulty in sawing, excessive distortion in seasoning, resistance to nailing, and poor working properties can be overcome at a cost that will allow such wood to be used for construction and joinery (Hughes 1968b). Furthermore, the increased use of wood for pulping may not encourage management of forests of poor-quality species. To operate efficiently, paper and board industries require raw materials of uniform size and quality. Into the distant

future, demand for large trees will continue because the strength and surface of their wood provide great versatility in the natural state, requiring little modification (Hughes 1968b).

Because the more valuable forest products are appraised according to dimension rather than weight, their economic productivity is more meaningfully expressed in volume growth (cubic meters per hectare per year) than in mass. However, where conversion is required, average wood specific gravity in primary moist tropical forests is about 0.6; therefore, for broad comparisons, 1 t metric equals about 1.67 m³, or 1 m³ equals about 0.6 t.

Only a small proportion of the wood in primary forests has generally been usable. Baur (1964b) found an average yield of usable wood of less than 3 m³/ha/yr. Ovington (1972) found a range from 2 to 6 m³/ha/yr, with the average below 3.5. Maudoux (1958, quoted by Catinot 1974) also gives an annual rate of growth for west African forests of 3 m³/ha/yr. Veillon (1974) found, in Venezuela, growth of 9.3 m³/ha/yr in a tropical moist forest, 4.0 in a tropical dry forest, and 1.0 in a tropical very dry forest. Mangroves in Madras, India, although subject to intensive demand, were once reported as producing no more than 2 m³/ha/yr of usable wood (Venkatesan 1966).

Assuming that the growth of individual trees may be expanded to the limit of forest growth in basal area, Dawkins (1961b) theorized that potential productivity of timber from native species would reach a maximum of 24 m³/ha/yr for lowland tropical forests. For rapidly growing, intolerant genera such as *Ochroma* and *Cecropia*, the maximum might reach 43 m³/ha/yr. However, such levels are not attainable with our present knowledge of site values and without genotypic selection. Moreover, present standards for sawlogs and veneer logs leave at least 40 percent of the stemwood volume unused.

If Dawkins' and Weck's prediction of a maximum stemwood productivity of 11 t/ha/yr is correct, if mean wood specific gravity is 0.6 and if current stands are producing only 3 m³/ha/yr (Baur 1964a), only about a sixth of the wood produced is considered marketable. Much more complete utilization of primary forests seems probable. Whitmore (1980) lists many of the products that could (and should) be made from the primary and secondary plants of the forests of Southeast Asia: timber, cellulose,

lignin, hemicellulose, protein, insecticides, essential oils, food colorings, medicines, gums, latexes, resins, and waxes.

Variations. The variability of tropical forests, even within short distances, probably greatly affects productivity but is difficult to characterize, assess, map, or predict. One example is the extremely variable rain forest in hill country where most of the large trees are on the ridges and upper slopes, such as in Malaysia and the West Indies (Burgess 1970, Wadsworth 1953). Yet, classification of subformations or associations over extensive areas, however convenient, remains nebulous because the classes may be arbitrarily defined sections of a continuum (Baur 1964a, 1964b). Discrete grouping seldom appears (Schulz 1960). In what appears an act of desperation, even the understory has been suggested as a site indicator superior to the overstory trees.

Description of the differences among tropical forests is difficult, and the results are not very satisfactory. The mere problem of tree identification may be almost insurmountable at the outset. Ecologists and botanists have come to question some of the identifications in the large transect study of the Amazon forests made by Heinsdijk (1960), something to be expected as botanical exploration and taxonomic research intensifies. Many species are rare. Also, juvenile foliage may be unlike that of mature trees. There is little outward evidence of the environmental adaptation of tropical trees or the periodicity of their functions, many flowering and fruiting nonsynchronously.

Low maximum stand density (basal area) is a striking limitation in tropical forests. The vertical stratification of crowns in a primary forest does not necessarily increase stand growth, even though it may increase growth of individual trees (Assman 1970). For mixed broadleaf forests, the maximum stand basal area that allows for acceptable, individual tree, diameter growth is generally less than 35 m²/ha, or about half that of Temperate Zone conifer and eucalypt forests. Crown diameter-to-d.b.h. ratios of 21 to 23 are common (Bell 1971, Pajmans 1970).

Dawkins reports that these ratios for light demanders, unlike those for tolerant species, do not decline as maturity is approached. The relatively open stand required to assure continued rapid growth of light demanders contrasts sharply with primary forests. The fact that respiration rates rise with temperature more rapidly than

photosynthesis rates (by the C³ path) may also limit the production of tropical forest ecosystems.

Primary forests contain many species that are difficult to assess, utilize, or grow. Examples are the *Calamus* spp., or rattans, which grow as a vine reaching the top canopy. Other species that are difficult to grow economically in mixed forests are those producing elastomers, resins, latexes, edible oils, medicinal products, and fruits. Many of the large trees of good form have extremely hard wood or high silica content. Some have low resistance to splitting. Others emit unpleasant odors or are a source of allergies. Many are of poor form or are so rare that not enough raw material is available for economic utilization.

The breadth of the niche utilized by each species is not obvious, leaving in doubt the causes of variation in species occurrence and performance. The presence of high buttresses and the lack of growth rings as reliable indicators of the age of woody species are major handicaps in assessing growth. Photogrammetry and other remote sensing techniques have not yet provided many details of silvicultural significance. Variations in tolerance by both species and age classes complicate growth predictions and silvicultural prescriptions. Merchantability of even apparently sound trees is highly variable because of hidden defects.

Trenching and understory weeding experiments shed light on the significance of competition for water and nutrients on individual tree growth within forest ecosystems. An experiment in a *Shorea* (deciduous) forest in India showed that weeding stimulated seedling height growth more than trenching did, the difference being highly significant (Bhatnagar 1959). In the weeded plots, trenching barely affected subsequent growth. This was unexpected because, in deciduous forests, competition from large trees was presumed to be more severe than competition from weeds. At the end of 12 months, trenching increased height growth 8 percent, compared with 39 percent for weeding. Because weeding should reduce competition for both water and nutrients, the two were probably confounded in the study. Also, the full benefits from trenching might not appear within 12 months.

Variations in growth times and rates among different species and in different places may be difficult to assess, let alone predict. Periodicity of growth in wet forests is largely independent of obvious climatic events

(Tomlinson and Gill 1973). Some species grow continuously, at least to some degree, and others exhibit periodicity of different degrees, making it necessary to measure growth in complete years. Even measuring only in the dry season is not safe for all species, because some that appear seasonal may grow even at this time (Longman 1969). Some species produce new leaves in the dry season. In Ghana, on the other hand, deciduous trees lose their leaves in November; whereas the predominantly evergreen trees tend to lose theirs in March (Longman 1969).

Not only is growth variable, but attempts to measure it can be confounded by seasonal shrinkage. Daubenmire (1972) found in Costa Rica a d.b.h. change of 0.04 cm in *Swietenia macrophylla* due solely to changes in bark moisture. Much larger differences have been recorded with *Eucalyptus robusta*, a species with spongy bark. Dry-season shrinkages in d.b.h. have been recorded up to 0.246 cm (Daubenmire 1972). Repeated growth measurements in successive dry seasons may vary significantly because of differences in dryness among seasons.

Growth rates may vary even during each day. Terminal growth of *Dendrocalamus strictus*, a bamboo, was determined for six culms averaging 137 cm in height (Dutta and Tomar 1964). New culms were produced from July to September. The maximum height growth for the six culms was 27.2 cm in a 24-hour period, but more than half the height growth occurred at night. In Suriname, measuring trees between 6:30 and 11 a.m. minimized daily variation (Schulz 1960).

The absence of clearly discernible growth rings and their unknown periodicity further complicate assessing tree growth rates in tropical forests. Most species do not produce rings sufficiently distinct and continuous to yield the same count by different observers. Even deciduous trees distinctly seasonal in stem-diameter growth may show little evidence of rings in the wood. Where growth rings are distinct, some correspond to shoot elongation, and some do not (Tomlinson and Gill 1973). *Avicennia germinans*, a mangrove, produces rings of such uniformity in separation that they correlate with stem diameter rather than age, and there apparently may be as many as six per year.

A 36-year record of the mean basal-area percentage growth of 153 trees of *Dacryodes excelsa* in an uncut, old-growth, subtropical wet forest in Puerto Rico recovering from a 1932 hurricane showed wide variation even when averaged for different periods each of several years. No readily evident explanation for the fluctuations exists, although the general tendency toward slower growth probably reflects increasing forest density with recovery. Clearly under these conditions, averages for even a few years may not represent the long term. The means are as follows:

Period	Mean annual Basal-area growth (%)
1946–82	2.04
1946–52	4.52
1952–58	2.42
1958–65	3.20
1965–76	1.42
1976–82	1.63

Assessing seed adequacy for sustaining stable tropical forest ecosystems is complicated by extreme variation among species in time of seedfall and in seed viability on the forest floor. Seeds of typical overstory species of wet forests are generally perishable and so may be present for only a brief period after they fall. Light-demanding genera such as *Cecropia*, on the other hand, may be minor components of primary forests, yet most of the viable seeds on the forest floor are theirs because of their long viability. These seeds may be dormant until some unusual event exposes them to enough light for germination, whereas germination of seeds of the tolerant species actually may be inhibited by light (Baur 1964a, 1964b).

Much has been said here about yields of harvestable products from primary forests. Such forests are still the chief source of forest products in many tropical areas. Yet, the removal of either plant or animal products from forests leaves a forest that, by definition, is no longer primary. If primary forests are to persist, their uses must be solely nonextractive, such as for preservation of plant and animal biodiversity and germplasm, soil stability, water quality, nonmanipulative scientific research, and nondestructive educational or recreational activities. Products, therefore, must ultimately come entirely from forests that are secondary and from plantations, discussed in the following chapters.