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JOHN J. EWEL[1], PAUL CHAI[2] AND LIM MENG TSAI[3]

Summary

The aboveground biomass and woody-plant floristic composition of three forests that had regenerated after logging followed by shifting cultivation were measured. Two of the forests were 4.5 yr old: one was on relatively good alluvial soil and the other was on a poorer — and more typical — upland soil. The other forest was 9.5 yr old, and was on an intermediate-quality site. The young forest on alluvium had about 5.4 kg m^{-2} of aboveground biomass: an amount that compares favorably with similar-aged plantations. The other young forest had only about 2.1 kg m^{-2} and the older stand had a mean of 3.9 kg m^{-2}. Most biomass on all three sites was accounted for by tree stems. High vine biomass was not always correlated with low tree biomass. Leaf biomass was relatively constant among sites and among plots within sites: about 0.5 kg m^{-2}. Fast-growing pioneer trees genera (*e.g. Macaranga, Ficus, Dillenia, Callicarpa*) accounted for most biomass at all sites, and may be typical of the kind of resource available in second-generation tropical forests. All three stands had relatively diverse understories of woody plants (mean of about 43 taxa per 300 m^2), and the young forest on alluvium was more species-rich than the two stands on poorer soils. Site quality is an extremely important factor; it governs both productivity and stand composition, and cannot be ignored in managing degraded tropical lands.

Introduction

Logging followed by shifting cultivation is one of the most common primary-forest conversion syndromes in the humid tropics, especially in Southeast Asia. The short-term importance of logging and shifting agriculture in Sarawak cannot be denied: forest products are an important earner of foreign exchange, and shifting agriculture feeds about a quarter of a million inhabitants. Even with its relatively low population density of about 12 persons per km^2, 65,000 to 120,000 ha undergo shifting agriculture each year, and >23% of the land in the State has undergone at least one agriculture cycle (Hatch and Lim, 1979). Foresters are often charged with the difficult task of rehabilitating and managing lands degraded by logging followed by shifting agriculture. Some of the problems involved were summarized by the participants in the 1978 workshop on shifting cultivation in Sarawak:

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> *"...land (used for shifting cultivation) rapidly revegetates after cutting and burning but generally with very poor quality secondary forest that is of little or no commercial value. Moreover, such secondary forest does not rapidly develop into good primary forest where the valuable hardwood timbers are once again present."* (Hatch and Lim, 1979, p. 13)

If degradation is not severe, if clearings are small, and if seed sources are present, forest recovery can be rapid and the second-growth forest is likely to contain a good stocking of tree species. Kochummen (1966) documented just such as example in Peninsular Malaysia. Where site degradation has been severe and seed sources are absent, however, succession is retarded and decades may elapse before a broad array of tree species becomes established (Gómez-Pompa *et al.*, 1972; Kochummen and Ng, 1977).

Most foresters faced with the management of such degraded lands opt for plantation establishment, but the establishment, maintenance, and protection of artificially regenerated forests are expensive forestry practices. There may soon be an alternative. Currently available technology permits the utilization of many more tropical species than was the case a few decades ago (*e.g.* see 16 articles in: Forest Products Laboratory, 1978, pp. 259–517). If world demand for cellulose continues to increase, tropical foresters may soon be able to concentrate on maximizing biomass production, rather than having to concern themselves with species composition. If so, soil seed banks and natural seed dispersal may produce adequate stocking of fast-growing species, and foresters might be free to emphasize silvicultural practices that influence stem form and productivity (Ewel, 1981).

Stand age is obviously related to biomass and species composition, and is the variable most often emphasized in studies of secondary forest structure (*e.g.*, Bartholomew *et al.*, 1953; Ewel, 1971; Snedaker, 1980; Zwetsloot, 1981). However, site quality is also an important — but often neglected — factor that influences regrowth quality (Harcombe, 1977; Aweto, 1981; Uhl, 1982; Uhl *et al.*, 1982). Therefore, we undertook a study of young secondary forests of two ages on three soils to determine the relative influence of time and site quality on stand composition and biomass.

Study sites

The study was conducted in the Sabal Forest Reserve, First Division, Sarawak, 114 km SE of Kuching, at 1°03′ N and 100°50′ E. The study area was at elevations of 25 to 45 m, in the foothills of the Klingkang Range, which forms the boundary between Sarawak and Kalimantan, Indonesia. The general area is underlain by sedimentary rocks of the Silantite Formation, and most of the area in the vicinity of the study sites is underlain by interbedded shales, mudstones, and silt stones (Leichti, 1960; G. Butt, pers. comm.). These parent materials often yield relatively light-textured deeply weathered, nutrient-poor soils (see Andriesse, 1972). Long-term (17 yr) mean annual rainfall at Sungai Pinang, 6 km from the study site, is about 4200 mm (Drainage and Irrigation Dept., 1981, plus 1980-data update). Mean monthly rainfall is 200 to 300 mm from May through August (the driest months), and >400 mm from November through February; other months receive 300 to 400 mm. The original vegetation was mixed dipterocarp forest. Agriculture can be sustained here only by intensive management — if at all — and the most appropriate land use for the area is probably forestry.

Vegetation was sampled at three sites, each of which had been tractor-logged (46 cm dbh limit), then subjected to a single shifting cultivation cycle. The unauthorised shifting cultivation was done by local Iban people, whose agricultural practices have been described by Freeman (1955). The main crop was upland rice, and in this area site preparation in July – August is followed by harvest in January – February. Two of the three sites had vegetation dating from the 1977 – 78 planting season, and the other had vegetation that grew after the 1972 – 73 season. Our sampling was done in April – May, 1982, which was 4 yr 3 mo after rice harvest at two sites and 9 yr 3 mo after harvest at the other. However, because some regrowth starts prior to harvest during the 6 mo rice-growing season, we refer to the vegetation ages as 4.5 and 9.5 yr.

The two 4.5-yr-old vegetations were on opposite edges of the same shifting cultivation clearing, about 0.5 km apart. Although they contained vegetation of exactly the same age and had identical site histories, they occupied strikingly different soils (Table 1; nomenclature after Lim, 1975). One site was on good soil: yellowish brown to dark brown recent alluvium, subject to wet-season flooding for brief intervals. The vegetation was tall (12.2 m), and one could easily walk through the understory. The soil auger struck charcoal at 90+ cm, indicating that a root may have burned to that depth or, more likely, that the site may have been subjected to agriculture before modern times. The other site, on a slope, was on poor soil: brownish yellow to yellow, developed *in situ,* and nutrient-poor. The vegetation on this poorer soil was only 6 m tall, and the vine-dominated (primarily *Dicranopteris*) understory was dense and almost impenetrable. The slope site was representative of a much larger area in the Sabal Forest Reserve than was the site on alluvium.

The 9.5-yr-old vegetation occupied a site where soil and topography were more heterogeneous than at either of the 4.5-yr-old sites. The yellowish brown to brownish yellow soil had been formed in *in situ,* and was probably intermediate in quality between the soils beneath the two 4.5-yr-old vegeta-

Table 1. Descriptions of the soils at the three study sites

4.5-yr-old vegetation on flat terrain; Recent Alluvium, Bemang family		4.5-yr-old vegetation ±10° slope, slightly undulating; Red Yellow Podzolic, Merit or Bekenu family		9.5-yr-old vegetation, 10–12°, midslope; Red Yellow Podzolic, Bekenu family	
Depth (cm)	Description	Depth (cm)	Description	Depth (cm)	Description
0.5–0	Irregular scattered litter, mostly leaves.	2–0	Dark brown (7.5YR 3/2) LFH; abundant fine and very fine roots; gradual but irregular (or broken) boundary to:	1–0	Scattered litter with irregular and discontinuous surficial fine and very fine root mat.
0–10	Dark yellowish brown (10YR 3/4), loam with abundant fine roots; friable; greasy; distinct smooth boundary.	0–4	Dark brown (7.5YR 3/2), A_1, silty loam; abundant fine roots; loose to friable; greasy; clear, wavy boundary into:	0–10	Yellowish brown (10YR 5.5/4) fine sandy loam; plentiful fine and very fine roots; friable.
10–20	Dark yellowish brown (10YR 4/4); fine sandy clay loam; few fine roots; friable; no mottles.	4–10	Brownish yellow (10YR 6/6) fine sandy clay loam; plentiful fine roots; few medium light grey (10YR 7/2) mottles; moderately firm.	10–25	Brownish yellow (10YR 6/7) fine sandy clay loam; plentiful fine and very fine roots; abundant light grey (10YR 7/1 and 7/2) mottles; friable.
20–35	Dark yellowish brown (10YR 4/4); fine sandy loam; very few roots; friable; no mottles.	10–35	Yellow (10YR 7/6) fine sandy clay loam; few fine roots; (few buried medium, dead roots); few fine light grey (10YR 7/2) and medium, distinct grey (10YR 5/1) mottles; moderately firm.	25–40	Brownish yellow (10YR 6.5/7) fine sandy clay loam; few fine roots; plentiful medium light grey (10YR 7/1 and 7/2) mottles; moderately firm.
35–50	Dark brown (10YR 4/3); fine sandy clay loams; very few fine roots; friable; no mottles.	35–50	Yellow (10YR 7/6) fine sandy clay loam; no roots; mottles as above; firm.	40–60	Brownish yellow (10YR 6.5/7) fine sandy clay loam with few coarse pockets of reddish yellow (7.5YR 6/6) fine sandy loam; no roots; plentiful medium light grey (10YR 7/1 and 7/2) mottles; few (±5%) angular to subangular gravel (lithic sandstone?); moderately firm.
50–65	Dark brown to brown (7.5YR 4/4); fine sandy loam; no roots; few fine reddish brown (5YR 4/4) mottles and few, coarse reddish grey (5YR 4/2) tinges; friable.	50–65	Yellow (10YR 7/6) fine sandy clay loam; no roots; abundant fine reddish yellow (7.5YR 6/6) and plentiful medium light grey (10YR 7/2) firm.	60–75	Brownish yellow (10YR 6.5/7) fine sandy clay loam few coarse pockets of reddish yellow (7.5 YR 6/6) fine sandy loam; no roots; plentiful (10–20%) subangular gravel (lithic sandstone); moderately firm.
65–80	Dark brown to brown (7.5YR 4/4) fine sandy clay loam; no roots; no mottles; moderately firm; moist.	65–80	Yellow (10YR 7/6) fine sandy clay loam; no roots; plentiful coarse light grey (10YR 7/2 and 7/1) mottles and fine reddish yellow (7.5YR 6/6) mottles; firm.	75–90+	Light brownish yellow (10YR 6.5/4) fine sandy clay loam; no roots; plentiful gravel; plentiful medium, light grey (10YR 7/2) mottles; moderately firm.
80–90	Drak brown to brown (7.5YR 4/4) fine sandy clay loam to fine sandy clay; no roots; moderately firm; no mottles; moist.	80–90+	Yellow (10YR 7/6) fine sandy clay to clay; no root; plentiful medium light grey (10YR 7/2) mottles; very firm.		
90+	Brown (7.5YR 4.5/4) fine sandy clay loam to fine sandy clay; no roots; no mottles; med. firm; moist few medium to coarse buried charcoal.				

tions. One of the sample plots at this site (No. 2) showed evidence of having been traversed along its upper quarter by a log-skidding trail. Two of the three plots were convex, but the third (No. 3) was concave, and may have received some sediment inputs from upslope erosion. The vegetation at this site was also heterogeneous. Tree heights averaged about 11.5 m. Many individuals of one tree species (probably a *Macaranga*) had died within the past year, creating sizable gaps in the canopy. These dead trees were enumerated, but not weighed, as part of the biomass harvest. The understory varied from open to very dense.

Methods

At each site a 90 m baseline was surveyed and three plots were located by randomly selecting distances along it. However, plots that would have either been within 5 m of another plot or traversed by a stream were not used, and new random selections were made to replace them. In the 4.5-yr-old vegetation on alluvium and in the 9.5-yr-old vegetation the plots were assigned to randomly chosen sides of the baseline, and were located 8 – 12 m from it. In the 4.5-yr-old vegetation on the slope the baseline was an abandoned skid road that ran down a ridge crest, and all plots were located on the same east-facing slope, 20 m from the ridge line.

Sample plots were 10 by 10 m, except in the 4.5-yr-old vegetation on the slope where plot size was reduced to 8 by 8 m because the trees were small, and the undergrowth was dense and homogeneous. After surveying, plot boundaries were marked with cord and the vegetation along the outside boundary was carefully cleared. Vines were cut where they crossed the plot boundary; all other plants were considered to be inside the plot if they were rooted within the plot, and outside if they were rooted outside, regardless of the location of their branches and foliage. Alternate borderline plants were designated as inside.

Before biomass harvesting began, a list of most of the plant species present was made. After harvesting opened up the understory of each plot, the girth (to 0.1 cm) and identity (at least to genus) of all trees $\geqslant 2$ cm dbh were recorded. Upon felling, the heights of the five tallest trees per plot were measured.

All aboveground biomass was harvested, and separated into three life forms: (1) herbs and shrubs, (2) vines (including climbing ferns, woody climbers, and herbaceous vines), and (3) trees. The tree category included all species that were capable of attaining a dbh of 5 cm at maturity, regardless of their size at the time of harvest. Each of the life forms was further separated into leaves and stems. Large petioles (*e.g.* those of *Macaranga* spp.) and most rachises of large, compound leaves were categorised as stems. No harvesting or weighing were done when leaf surfaces were wet with rain. Flowers and fruits from all three life forms were combined and weighed as a single category. Roots, litter, and standing dead organic matter were not harvested.

Fresh weights were measured (to 10 g) in the field, immediately after separation of leaves and stems (Salter 235 dial balance, 25 kg x 100 g). Subsamples (grab samples of ca. 0.5 kg of leaf or 1.0 kg of stem) for oven-dry weight determination were taken immediately atfer weighing, and subsample fresh weights were measured (to 0.1 g) in the field (Ohaus triple beam balance, 2610 g x 0.1 g). Usually, three subsamples of each category (*e.g.*, vine stems, tree leaves, *etc.*) were taken from each plot. However, on two of the plots in the 4.5-yr-old vegetation on the alluvium and on the three plots in 9.5-yr-old vegetation, five subsamples of tree stem were taken. Also, only one subsample of flowers and fruits was taken from each plot.

Subsamples were stored in a field plant drier to reduce their moisture content and retard respiration until they could be transported to the laboratory, which was usually within 72 h after harvest. Subsamples were then oven dried at 150°C: stems for at least 72 h; leaves, and flowers and fruits, for at least 48 h. Oven-dry weights were recorded to 0.1 g. For each plot, the mean per cent dry weight of each category was calculated, based on the (usually) three subsamples of that category from that plot. The individual per cent dry weight values were usually within 5% of the mean per cent dry weight, but tree stems were sometimes more variable. The mean per cent dry weight of each category on a plot was multiplied by the total fresh weight of that category to determine oven-dry weight per plot.

Results

Biomass

The 4.5-yr-old vegetation on alluvial soil supported substantially more biomass (5.4 kg m^{-2}) than either the 9.5-yr-old vegetation (3.9 kg m^{-2}) or the 4.5-yr-old vegetation on the slope (1.7 kg m^{-2}) (Table 2). The biomass data were subjected to one-way analysis of variance, and significant differences ($p<0.05$) were detected using Duncan's Test (SAS, 1979).

The distribution of leaves among life forms (herbs and shrubs, vines, or trees) differed from site to site, but the total leaf biomass per plot was remarkably constant (mean = 0.5 kg m^{-2}), and did not differ significantly among sites.

The story for stem biomass, however, was quite different. Like leaf biomass, it varied greatly among compartments, but also varied greatly

Table 2. Biomass of successional vegetation at three sites

Values are g.m^{-2}, oven-dry weight.

	4.5-yr-old, Alluvium				4.5-yr-old, Slope				9.5-yr-old			
	Plot 1	Plot 2	Plot 3	Mean	Plot 1	Plot 2	Plot 3	Mean	Plot 1	Plot 2	Plot 3	Mean
Herbs and shrubs												
Leaves	54	38	31	41	250	89	192	177	46	87	112	82
Stems	71	26	24	40	587	280	688	518	96	192	235	174
Subtotal	125	64	55	81	837	369	879	695	142	279	348	256
Vines												
Leaves	102	78	116	99	42	175	99	105	134	96	49	93
Stems	551	392	571	505	79	450	136	222	161	130	179	157
Subtotal	653	470	687	603	121	625	235	327	295	226	228	250
Trees												
Leaves	274	464	276	338	121	392	101	205	366	314	296	325
Stems	5143	5169	2659	4324	706	1448	493	882	3265	2203	3866	3111
Subtotal	5417	5633	2935	4662	827	1840	594	1087	3631	2517	4162	3437
Total Leaves	430	580	423	478	413	656	392	487	546	497	457	500
Total Stems	5765	5587	3254	4869	1372	2178	1317	1622	3522	2525	4280	3442
Fruits and Flowers	6	15	9	10	10	<1	8	6	2	3	4	3
Grand Total	6201	6182	3686	5356	1795	2834	1717	2115	4070	3021	4742	3944

among sites and among plots. Due to high among-plot variation only the total stem biomasses of the two 4.5-yr-old vegetations differed significantly; the mean stem biomass in the 4.5-yr-old stand on alluvium was three times greater than that of the 4.5-yr-old vegetation on the slope (4.9 compared to 1.6 kg m^{-2}). Tree stems, as expected, accounted for most of the biomass on each of the three sites.

Although one usually thinks of vine growth as inhibiting tree growth, especially in young secondary forests, the 4.5-yr-old vegetation on the alluvium (*i.e.* the site with most tree-stem biomass) had significantly more vine-stem biomass (0.5 kg m^{-2}) than did the other two sites (mean of 0.2 kg m^{-2}).

The biomass of reproductive parts ranged from <1 to 10 g m^{-2} and did not differ significantly among sites.

Floristics and stocking

Most of the trees $\geqslant 2$ cm dbh, and most of the basal area, on each of the three sites was accounted for by fast-growing genera such as *Macaranga, Ficus,* and *Callicarpa* (Table 3). The young vegetation on alluvium was dominated by *Callicarpa pentandra* the young vegetation on the slope by *Macaranga conifera* and *C. pentandra;* and the older vegetation by *Macaranga hypoleuca.* The only dipterocarps $\geqslant 2$ cm dbh found were two species of *Shorea* in the upland, 4.5-yr-old vegetation.

The stocking decreased from a mean of about 3900 trees per ha in the 4.5-yr-old vegetation to about 2200 trees per ha in the 9.5-yr-old vegetation. This decrease would be expected as competition — both inter- and intraspecific — increases with stand age. This decrease in stocking was not, however, accompanied by the increase in basal area that might have been expected: basal area of the young stand on alluvium was substantially higher than that of the 9.5-yr-old stand (16.3 compared to 12.7 m^2 ha^{-1}). Basal area of the young stand on the upland soil was lowest of all: 4.3 m^2 ha^{-1}.

The small ($\leqslant 2$ cm dbh) trees and shrubs on the three sites included representatives of 42 families (Table 4). The two younger stands had about twice as rich a woody understory flora (mean of 52 taxa each, without correcting for the smaller plot size on the slope) as did the older stand (27 taxa). All sites, however, had a good representation of potentially useful tree species in the understory.

Discussion

The aboveground biomasses of the three study sites are compared to those of similar-aged forests elsewhere in the humid tropics in Table 5. In

Table 3. Trees ⩾2 cm dbh on the harvested plots

Only species with a total of ⩾3 individuals on the 3 harvested plots per site are enumerated. Plot size in the 4.5-yr-old vegetation on the slope was 8 by 8 m; others were 10 by 10 m.

Taxon	4.5-yr-old vegetation on alluvium		4.5-yr-old vegetation on slope		9.5-yr-old vegetation	
	Density (no./ha)	Basal area (m/ha)	Density (no./ha)	Basal area (m/ha)	Density (no./ha)	Basal area (m/ha)
DILLENIACEAE						
Dillenia reticulata			156	0.09		
Dillenia suffruticosa					167	0.33
Dillenia sumatrana			104	0.06		
DIPTEROCARPACEAE						
Shorea quadrinervis			104	0.06		
Shorea venulosa			260	0.37		
ELAEOCARPACEAE						
Elaeocarpus stipularis	133	0.59				
EUPHORBIACEAE						
Cleistanthus sp.	100	0.14				
Endospermum diadenum			104	0.11		
Macaranga conifera			677	0.53		
Macaranga gigantea			104	0.13		
Macaranga hosei	233	3.20			133	0.97
Macaranga hypoleuca	133	1.11			467	4.91
Macaranga trachyphylla					233	1.44

LAURACEAE						
Litsea ? castanea			156	0.13		
LOGANIACEAE						
Norrisia maior			104	0.16	100	0.63
MORACEAE						
Ficus bruneiensis	200	1.10				
Ficus bruno-aurata	200	0.27	208	0.29		
Ficus grossularioides			260	0.19	100	0.04
Ficus obpyramidata	467	1.43				
Ficus sp.	333	0.38			200	0.27
RUTACEAE						
Evodia alba					167	1.64
THEACEAE						
Adinandra dumosa					300	1.45
VERBENACEAE						
Callicarpa pentandra	933	6.18	469	0.43		
Others	1135[a]	1.81[a]	1354[b]	1.79[b]	334[c]	1.00[c]
TOTAL	3867	16.21	4060	4.34	2201	12.68

[a] Includes 13 families, 20 genera

[b] Includes 19 families, 22 genera

[c] Includes 5 families, 6 genera.

Table 4. Trees and shrubs <2 cm dhh on ⩾1 of the harvest plots at each site

Plot size in the 4.5-yr-old vegetation on the slope was 8 by 8 m; others were 10 by 10 m.

Taxon	4.5-yr-old vegetation on alluvium	4.5-yr-old vegetation on slope	9.5-yr-old vegetation
ANACARDIACEAE			X
Buchanania lucida		X	
Melanorrhoea sp.	X		
ANNONACEAE			
Goniothalamus sp.	X	X	X
Polyalthia sp.	X	X	X
Popowia sp.	X		
APOCYNACEAE			
Alstonia sp.			X
AQUIFOLIACEAE			
Ilex cissoidea		X	
Ilex cymosa			X
BOMBACACEAE			
Durio sp.	X		
BURSERACEAE			
Canarium sp.	X		
Dacryodes sp.		X	
CELASTRACEAE			
Bhesa paniculata	X		
COMPOSITAE			
Vernonia arborea	X		
DILLENIACEAE			
Dillenia suffruticosa			X
DIPTEROCARPACEAE			
Hopea sp.	X	X	
Shorea seminis	X		
Vatica sp.		X	
EBENACEAE			
Diospyros (2 spp.)	X	X	
EUPHORBIACEAE			
Antidesma sp.	X		
Baccaurea sp.	X		
Chaetocarpus castanocarpus	X		
Drypetes sp.	X	X	
Glochidion sp.		X	
Macaranga (2 spp.)		X	
Mallotus macrostachyus			X

Mallotus sp.	X		
Pimeleodendron griffithianum		X	
FAGACEAE			
Lithocarpus (2 spp.)	X		
GUTTIFERAE			
Calophyllum sp.	X		
Cratoxylum cochinchinense	X		
C. formosum	X		
Garcinia sp.	X		
Mesua sp.	X		
LAURACEAE			X
Alseodaphne sp.	X		
Eusideroxylon zwageri	X		
Litsea oppositifolia	X		
Litsea (2 spp.)		X	
Phoebe sp.	X		
LEEACEAE			
Leea aculeata			X
LECYTHIDACEAE			
Barringtonia sp.			X
LEGUMINOSAE	X		
Dialium laurinum			X
Millettia sp.			X
Pithecellobium borneense		X	
LOGANIACEAE			
Fagraea racemosa	X	X	X
Norrisia maior	X		
MELASTOMATACEAE			
Melastoma malabathricum	X	X	X
Memecylon sp.	X	X	
Pternandra sp.	X	X	X
MELIACEAE			
Aglaia sp.	X		
MORACEAE			
Artocarpus anisophyllus	X	X	
Ficus (2 spp.)	X		X
Ficus sp.		X	
MYRISTICACEAE			
Horsfieldia sp.	X		
Knema sp.	X	X	
Myristica sp.	X		
MYRTACEAE			
Eugenia (3 spp.)	X		
Eugenia sp.		X	X
OCHNACEAE			
Gomphia serrata		X	

OLACACEAE			
Chionanthus sp.		X	
POLYGALACEAE			
Xanthophyllum (2 spp.)	X		
Xanthophyllum sp.		X	X
PROTEACEAE			
Helicia sp.		X	
RHIZOPHORACEAE			
Anisophyllea disticha		X	X
ROSACEAE			
Parastemon urophyllum		X	
RUBIACEAE			
Canthium sp.		X	
Ixora sp.	X	X	
Lasianthus sp.	X		
Nauclea spp.	X	X	
Timonius sp.	X		X
Urophyllum hirsutum	X	X	X
Zeuxanthe prismatomeriformis			X
RUTACEAE			
Euodia nervosa		X	
SABIACEAE			
Meliosma sp.	X		
SAPINDACEAE			
Lepisanthus sp.		X	X
Nephelium sp.	X	X	
Xerospermum sp.		X	
SAPOTACEAE		X	
SAURAUIACEAE			
Saurauia sp.	X	X	
STERCULIACEAE			
Scaphium sp.		X	
Sterculia sp.	X		
SYMPLOCACEAE			
Symplocos sp.	X	X	X
THEACEAE			
Adinandra dumosa		X	X
TILIACEAE			
Grewia sp.	X	X	
ULMACEAE			
Gironniera subaequalis		X	
VERBENACEAE			
Vitex pubescens			X
TOTAL TAXA	56	47	27

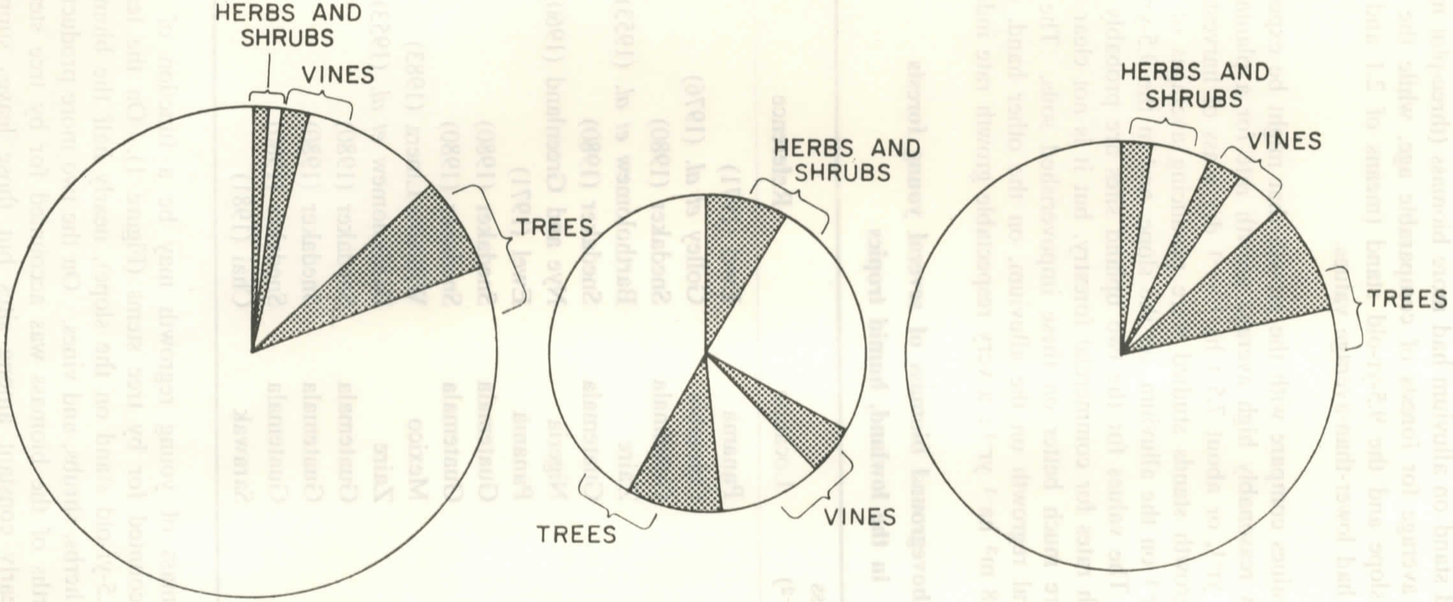
general, the 4.5-yr-old stand on alluvium had more biomass (three-plot mean of 5.4 kg m^{-2}) than average for forests of comparable age, while the 4.5-yr-old stand on the slope and the 9.5-yr-old stand (means of 2.1 and 3.9 kg m^{-2}, respectively) had lower-than-average values.

How do these values compare with the growth that might be expected from plantations? A reasonably high average growth rate for a plantation might be 30 m^3 ha^{-1} yr^{-1}, or about 7.5 t ha^{-1} yr^{-1} dry mass of harvestable stems. The second-growth stands studied were producing averages of 9.6, 2.0, and 3.3 t ha^{-1} yr^{-1} on the alluvium, on the slope, and in the 9.5-yr-old stands, respectively. The values for the two upland sites are probably unacceptably low growth rates for commercial forestry, but it is not clear that plantations would fare much better on these impoverished soils. The increment of the natural regrowth on the alluvium, on the other hand, corresponded to about 38 m^3 ha^{-1} yr^{-1}: a very respectable growth rate indeed.

Table 5. Aboveground biomass of several young forests in the lowland, humid tropics

Age (yr)	Biomass (kg. m^{-2})	Location	Reference
4	3.8	Panamà	Ewel (1971)
4	4.9	Colombia	Golley *et al.* (1976)
4	2.7	Guatemala	Snedaker (1980)
5	7.7	Zaire	Bartholomew *et al.* (1953)
5	3.7	Guatemala	Snedaker (1980)
6	4.6	Nigeria	Nye and Greenland (1960)
6	4.3	Panamà	Ewel (1971)
6	4.5	Guatemala	Snedaker (1980)
7	4.7	Guatemala	Snedaker (1980)
7	4.3	Mexico	Williams-Linera (1983)
8	12.2	Zaire	Bartholomew *et al.* (1953)
8	6.6	Guatemala	Snedaker (1980)
9	7.2	Guatemala	Snedaker (1980)
10	5.4	Guatemala	Snedaker (1980)
10 – 14	3.0	Sarawak	Chai (1981)

The usable biomass of young regrowth may be a function of the proportion that is accounted for by tree stems (Figure 1). On the least-productive site (the 4.5-yr-old stand on the slope), nearly half the biomass was accounted for by herbs, shrubs, and vines. On the two more productive sites, about three-fourths of the biomass was accounted for by tree stems. Leaf biomass was nearly constant among sites but those leaves support



4.5 YR-OLD, ALLUVIUM
(5.4 Kg · m^{-2})

4.5 YR-OLD, SLOPE
(2.1 Kg · m^{-2})

9.5 YR-OLD
(3.9 Kg · m^{-2})

Figure 1. Biomass distribution by life form at the three study sites. Values are means from three plots per site. Shaded segments are leaves; open segments are stems.

different kinds of stems. Herb and shrub stems are replaced with greater frequency than tree stems, so accumulate relatively little biomass. Vines rely on other plants for support, so they too accrue little biomass. If cellulose production is a primary management objective, it is essential to establish a good stocking of trees early, before the site is captured by life forms that produce less wood.

Almost all of the biomass of the sampled areas was accounted for by fast-growing pioneer species in the Euphorbiaceae, Verbenaceae, Dilleniaceae, and Moraceae (Table 3). Most such species have low-density wood and are relatively short-lived. One might expect the understory of young stands to eventually become colonized by shade-tolerant, longer-lived taxa more characteristic of older forest. With few exceptions, however, that expectation was not borne out by our data (Table 4): the young stands had more species-rich understories than did the older stand.

Four unmeasured factors may have accounted for the high species richness of the 4.5-yr-old stand on alluvium. (1) It was topographically low, so more kinds of seeds may have been dispersed onto it than onto upland sites. (2) It may have been nearer seed sources. (3) It may have had a larger, more diverse seed pool in its soil. (4) The combined effects of competition and environment may have permitted a greater diversity of species to survive here than on the upland sites. Why the 4.5-yr-old upland vegetation (topographically high, poor soil) should have had so many more species than the 9.5-yr-old stand is less easily explained, but may be related to factors 2 and 3, above, as well as to site history.

The alluvial soil clearly supported much more impressive vegetation — in terms of both biomass and species richness — than did the two upland soils. Good alluvial soil, however, is a relatively scarce commodity, and is likely destined for agriculture rather than forestry. Foresters will still be faced with the difficult task of management of relatively poor soils deforested by logging and shifting cultivation: typical of the kinds of sites where retrogression of succession is always a danger (Ewel, 1983). Plantations are one option but they are expensive and risky ventures. Where site quality is good and tree regeneration — even of pioneer species — is dense, natural regrowth offers another alternative that merits consideration.

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