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ECOLOGICAL STUDIES IN FOUR CONTRASTING LOWLAND RAIN FORESTS IN GUNUNG MULU NATIONAL PARK, SARAWAK

I. FOREST ENVIRONMENT, STRUCTURE AND FLORISTICS

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SUMMARY

(1) Gunung Mulu National Park, Sarawak, has an area of 544 km^2 and a wide range of rain forest formations on several soil types and at altitudes of 50–2376 m. It has an annual rainfall of about 5000 mm.

(2) Sites of 1 ha were established in each of four contrasting types of primary lowland rain forest: alluvial forest (AF); dipterocarp forest (DF); heath forest (HF) and forest over limestone (LF). All trees ($\geqslant$10 cm dbh) were measured for dbh and height, except for the LF where height was calculated using a regression equation based on height and diameter measurements of a sample of thirty-four trees. Estimates of numbers or biomass or both of small trees (< 10 cm dbh), lianes, ground herbs and ferns, and epiphytes (including ferns) $\leqslant$3 m from the ground were also made. Epiphytes > 3 m from the ground and bryophytes were not ennumerated. The total above-ground forest biomass (t ha^{-1} dry weight) was calculated as: AF, 250; DF, 650; HF, 470; LF, 380.

(3) Leaf and branch material were collected from each tree and, as far as possible, identified to species. There were at least 223 species ha^{-1} in the AF; 214 in the DF; 123 in the HF; and seventy-three in the LF.

(4) Soil analyses were carried out using standard methods on twenty-five samples from each site. The AF soil was heterogenous, with gley soils of high base status in the lower, occasionally flooded, part and podzols and peats in the higher part. The DF soil was acid and very low in calcium. It was lower in total exchangeable bases than the very acid podzolic soils of the HF. The LF soils were shallow, highly organic, of high base status, and neutral to mildly acid pH.

(5) It was demonstrated that the species-rich DF occurred on very poor soils but there was no simple relationship between soil nutrient element concentrations and biomass or species richness. Many factors are probably involved in controlling these attributes.

(6) The causes of the distinctive sclerophyllous leaves of the heath forest are discussed. It is suggested that extreme soil acidity (in the absence of a buffering effect of Al^{+++}) in the organic soils limits nitrogen mineralization and that low levels of biologically active nitrogen favour sclerophylly. Those features of heath forest which reduce transpiration may be important in reducing the mass flow of soil toxins to the root surfaces.

INTRODUCTION

Gunung Mulu National Park, Sarawak (henceforth called the Park) has an area of 544 km^2, most of which is covered by primary forest on many different soils and at altitudes from 50 m to 2376 m. Figure 1 shows its location. From June 1977 until September 1978 a floristic, faunistic and geomorphological survey was carried out by the joint Sarawak Forest Department–Royal Geographical Society Mulu Expedition. In addition an

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investigation was made of some features of decomposition and element cycling on sites in four contrasting lowland forests (Anderson, Proctor & Vallack 1983: Proctor *et al.* 1983). Whitmore (1975) had commented that there was little published information on these aspects for any tropical forests in the Far East and the Park offered an ideal study area.

Our main aim in this paper is to provide a background to this study of decomposition and element cycling. We describe some general features of the Park and give a detailed account of the structure, floristics, climate and soils (including the results of chemical analyses by standard methods) of four sites, each representing one of four forest types of Whitmore's (1975) forest formation classification.

Alluvial forest was formerly more widespread in Sarawak but much has been cleared for cultivation. The Park has some fine undisturbed examples developed mainly on alluvium, and innundated for a few days at the wettest times of the year. This forest type and the next are facies of tropical lowland evergreen rain forest which includes the most luxuriant of all plant communities and probably has the greatest number of species of any rain forest formation.

Dipterocarp forest is well represented in the Park on red-yellow podzolic soils. The Sarawak foresters call this forest 'mixed dipterocarp forest' which distinguishes it from those forests (e.g. the *Shorea albida* peat swamps of northern Borneo) where one dipterocarp species is dominant. However the name is not used elsewhere in the Far East and we use here the shorter name, dipterocarp forest.

Heath forest is often called by its Iban name of *kerangas.* It occurs on soils derived from siliceous parent materials which are low in bases and coarse textured. It is developed in many places in the Park on terraces which are probably of Pleistocene age. This forest has several distinctive characters: many trees with small, hard, glossy leaves; abundant bryophytes on the ground; many insectivorous plants and myrmecophytes. Forests of this type occur in many places in the Far East (except East Malesia) but are more extensive in Borneo than elsewhere and are associated with the formation of podzols or bleached sands. Brünig (1974) has provided a detailed monograph and classification of heath forests of Sarawak and Brunei. Some of the distinctive features of the heath forest are discussed later in this paper in relation to the soil analyses and other recent work.

Forest over limestone occurs frequently in the Park although only a small proportion is in the lowlands. Such forests are fairly common in South-East Asia and have been reviewed by Anderson (1965). Our study was restricted to the type he described as occurring at the base of cliffs and ravines.

For each of these four forest types one site of 1 ha (marked on the ground, not corrected for slope) was established. We use the following abbreviations for the sites: AF (alluvial forest); DF (dipterocarp forest); HF (heath forest); LF (forest over limestone). (It is explained later that part of the AF is sometimes treated separately and the abbreviation, GAF is used for this part.) Their locations and those of nearby permanent camps are shown in Fig. 1. The sites were chosen as being good examples of primary forest of each type. Three of the sites had almost no human disturbance. The DF included a plot of 0·4 ha described by Martin (1977) and there was some minor disturbance associated with his 1975 field work. The main Gunung Mulu path (about 1 m wide) runs through this site but was thought to have negligible impact on it.

This paper supersedes a preliminary account of some aspects of the work (Proctor, Anderson & Vallack 1982) in which the DF is called mixed dipterocarp forest and the HF is called kerangas.

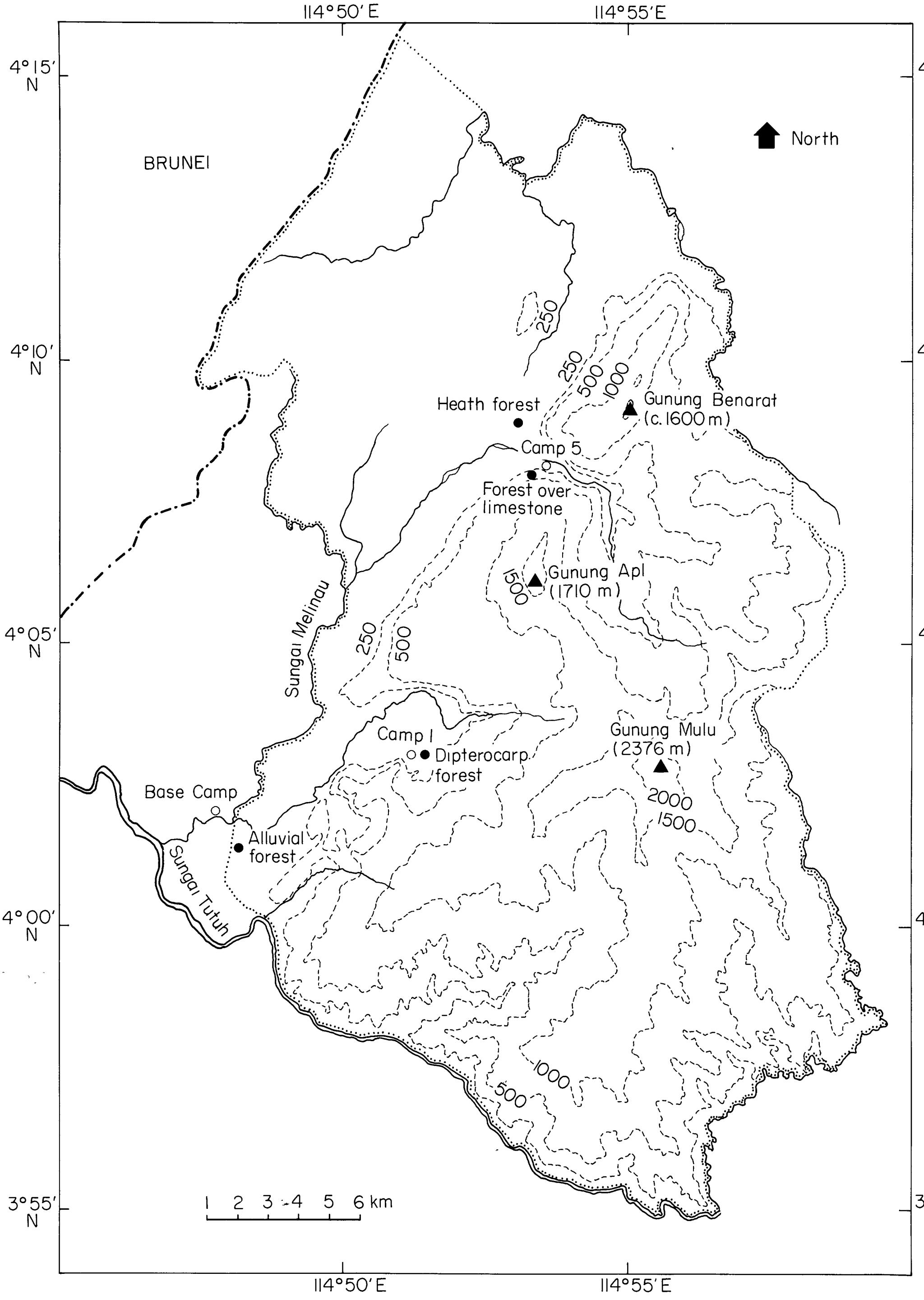

FIG. 1. The locations of Gunung Mulu National Park, Sarawak, with: (●), the lowland forest sites; (○), their nearest camps; ·····, Park boundary; —·—, international boundary with Brunei.

GEOLOGY AND GEOMORPHOLOGY

The geology and geomorphology of the Park have been described by Sweeting (1980). The area forms part of the large north-west Borneo geosyncline which is thought to have developed during the Upper Cretaceous period. The oldest sediments outcrop in the east of the Park and are the late Cretaceous–early Tertiary clastic deposits of the Mulu Formation. They are mainly argillaceous, although sandstones and quartzites are locally important. These rocks have been subject to intense deformation and some metamorphism, so that a range of shales, phyllites and slates occur. The beds form an anticlinorium with the flanks dipping to the north-west and south-west and with the apex near the summit of Gunung Mulu. The Mulu Formation is overlain on the north-western flank of the anticlinorium by the younger rocks of Melinau Limestone Formation. These are almost pure limestone and mostly calcitic (as at the LF) although dolomites are locally important.

The topography of the Mulu Formation and Melinau Limestone Formation outcrops is mountainous and rugged. The main summit tower of Gunung Mulu (2376 m) is formed from the slates at the core of the Mulu anticlinorium. This peak and the five major radiating ridges with their subsidiary spurs dominate the topography of the Mulu Formation in the Park. Many of the soils on Gunung Mulu (as in the DF) are developed on colluvial parent materials (Tie *et al.* 1979).

The flat ground in the Park is occupied by extensive alluvial deposits (as at the AF) and terraces of different heights which have been described by Woodroffe (1980). The HF occurs on a medium-height terrace of coarse sandy deposits probably of Pleistocene age.

CLIMATE

The climate of the Park has been described by Walsh (1982) and the following account is based almost wholly on his paper.

The Park's climate is controlled largely by the Indo-Australian monsoon system: the north-east monsoon from December to March and the south-west monsoon from May to October. During the transition periods, winds are variable and near-equatorial troughs and associated disturbances affect the region. Tropical cyclones do not affect the area. Rainfall usually occurs in the form of convectional showers, generally in the afternoon or night. Although rainfall occurs in all months of the year there is a peak after each equinox (in October–November and April–May) during the transition period between the two monsoon systems. The rainfall remains high during the north-east monsoon; the south-west monsoon, particularly July–September, is drier because the air has passed over the land mass of southern Borneo.

Walsh (1982) has summarized rainfall records from 1 September 1977 to 31 August 1978 for gauges located at permanent camps near the four sites (Fig. 1). The annual rainfalls were: for Base Camp, 5090 mm; Camp 1, 5110 mm; Camp 5, 5700 mm. (The monthly values for these camps are shown in Fig. 1 of Proctor *et al.* 1983.) At Base Camp only 99 mm fell in September 1977 and 134 mm in August 1978; all other months had more than 250 mm.

Daily records were kept at Base Camp. Rain fell on 275 days, with over 2·5 mm on 226 days of the year. Falls of 25 mm or more occurred on 66 days. There were seven falls of 76 mm or more in a 24 h period; the greatest was 187 mm on 2 November 1977. These heavy falls were concentrated in the peak wet months. In the drier season there were 16 days with no rainfall in August 1977, 15 in September 1977, and 15 in August 1978.

The Park has high, even temperatures; seasonal variations were minor. Daily Stevenson screen temperature records were made at two localities near Base Camp: in a clearing of about 3000 m^2 on the bank of the Sungai Melinau; and under the canopy in an old secondary forest which resembled the AF. In the clearing, minimum temperatures occurred around dawn and were nearly always between 20·6 °C and 22·8 °C. The lowest temperature recorded was 19·9 °C in January 1978. Maximum temperatures showed greater variation. In clear sunshine, sustained until at least noon, temperatures usually rose to 32·2–33·9 °C; on overcast and rainy days, temperatures rose to 26·7–30·0 °C. The highest maximum recorded was 35·0 °C on 24 September 1977 during exceptionally dry weather. The number of days which were cloudy or rainy throughout was very small. In the secondary forest the diurnal ranges were lower (5·0 °C) than those in the clearing (9·7 °C). The maximum temperatures were much lower in the forest, but minimum temperatures were almost the same as in the clearing. On sunny days maxima in the forest reached 26·7–28·9 °C and on rainy, overcast days 25·6–26·7 °C. Mean temperatures in the forest were about 2·2 °C lower than those recorded in the clearing. (Data for the forest site are summarized in Fig. 1 of Proctor *et al.* 1983.)

The DF, HF and LF are at higher altitude (200, 170 and 300 m respectively) than the AF and Base Camp (50 m) and would be expected to be a little cooler. The lapse rate on Gunung Mulu is about 5 °C per 1000 m (calculated from the data in Walsh 1982).

No systematic observations on wind or evaporation have been made. Walsh (1982) noted that wind speeds in the lowlands of the Park are generally low and suggested that, in north-eastern Sarawak, annual evaporation is of the order of 1500 mm. Evapotranspiration losses have been shown (Brünig 1971) to vary immensely with vegetation type and structure in Borneo, and such variations will certainly apply in the Park.

SOILS AND TOPOGRAPHY

Tie *et al.* (1979) carried out a soil survey of the Park including our sites. The following description draws largely from their account and is combined with topographic surveys (C. Woodroffe, unpublished) for the AF and HF and our own soil and topographic surveys for the DF and LF sites. The soils are classified by the system of Lim (1975).

Alluvial forest site

The 100 × 100 m site is at an altitude of 50 m and is fairly flat with the highest point about 3·3 m above the lowest. This height difference is very important because of its relation to flooding frequency and soil type. The lower parts of the site were inundated on three occasions (for about 24 h each) between 1 July 1977 and 1 September 1978.

On the lower flat ground, the drainage is poor and gley soils of the *Bijat* family occur. The water table generally occurs close to the surface and even after a dry period in late August 1978 the water table near the lowest part of the site was only at 55 cm depth. The A horizon usually consists of dark greyish-brown, friable loam to silty clay loam. The subsoil is a grey clay often with some sand and gravel below 60 cm depth. The *Bijat* family soils here are of higher pH and base saturation than those of the same family elsewhere in Sarawak. This results from the calcareous flood-waters of the Melinau River which drain much of the Park's limestone. The highest ground in the AF is probably a low terrace remnant and has weak incipient humus podzols of the *Buso* family. In these, gravel beds are encountered at depths of 20–40 cm. A thin layer of illuviated organic material is found just above the gravel beds or around the pebbles or both. The top soil is a pale loamy sand to sandy loam. Where drainage has been impeded, a thin layer of peat has accumulated on top of the humus podzol and in one area organic soils (> 50 < 100 cm deep) of the *Mukah* family occur. These *Mukah* soils have a layer of reddish brown, moderately well-decomposed humic materials overlying dark, yellowish brown, silty clay loams or silty clays. There is a small area of grey-white podzolic soils of the *Saratok* family which are developed on slightly heavier-textured terrace materials.

We have called the lower part of the site the 'gley-soil part of the alluvial forest' (GAF). Some information is presented separately for this area since it is on a distinctive uniform soil and probably represents the true alluvial forest or 'empran' of Browne (1955).

Dipterocarp forest site

The site ranges from about 200 to 250 m altitude and occupies the crest and flank slopes of the lower end of an intermediate spur from the west ridge of Gunung Mulu. The spur is interrupted by a saddle which divides the site into an upper part 100 × 20 m (0·2 ha) and a lower part (about 0·8 ha) 220 m long and varying in width (with the flatter parts of the spur) from 20–40 m. The slopes of the flanks are mostly 15–20° and the total site area on a horizontal projection is 0·95 ha.

The soils are heavy-textured red-yellow podzolics with a surface layer (up to about 15 cm thick) of reddish-brown fibrous organic matter. The upper mineral horizon is darkened by organic matter and colours range from dark brown to yellowish brown. (Very locally there are some patches of grey or light grey, indicating either intensification of leaching or hydromorphism.) This horizon is generally less than 15 cm deep, and gives way to the reddish-yellow or yellowish colours of the subsoil. In general the colour becomes redder with depth but there is considerable range in subsoil matrix colours including mottled patches of incomplete weathering. The topsoils commonly have silty loam or very fine sandy loam textures, but clay contents increase with depth, and silty clay loams or heavier clays are usually found within 15 cm of the surface. Topsoil structures are weak or moderate medium crumb or fine subangular blocky. Subsoil structures are usually medium or coarse blocky, but may be obscured in horizons with high contents of weathering rock fragments. The stone content generally increases with depth, but not in a gradual or regular way. Slightly weathered rock is usually abundant at 100–200 cm depth.

The soils are mainly of *Merit* and to a lesser extent *Tutoh* families. In the *Merit* family, the horizons are more strongly developed and the increase in clay and stones is quite marked. *Tutoh* family soils are developed on more recently deposited colluvial parent materials, and show less marked horizons.

There are some features of these soils which are not typical of red-yellow podzolic soils in Sarawak. The surface organic matter layers are unusually thick and similar to those more often found in light-textured soils. On heavy-textured soils, surface organic matter is usually less than 2 cm thick and is often absent. This sandstone feature in the soils of the DF together with some unusual floristic composition of the forest is anomalous and is discussed later. The soils are deeper than most Sarawak red-yellow podzolic soils in similar situations, probably as a consequence of colluvation and the long catchment slopes above.

Heath forest site

This 100 × 100 m site occurs at about 170 m altitude on a medium-height terrace of sandy deposits (Woodroffe 1980). There is about 2 m difference in height between the highest and lowest points. The soils are mainly humus podzols of the *Miri* family which has an indurated B_h horizon. Some *Buso* family soils were also found where the humus pan is less indurated and is penetrable with an auger.

In less well drained parts (the humic pan is the main cause of the poor drainage), these humus podzols have a peaty surface. Locally, deep *Anderson* family organic soils of 100–150 cm of reddish-brown peat are found. The HF resembles type 512·14 in Brünig's (1974) classification of heath forests and is similar to his sample plots from the Mulu area (Brünig 1968).

Forest over limestone site

This site is situated at about 300 m altitude and is on a mainly 25–30° slope on the northern side of the Gunung Api massif. The site is 160 × 60 m (plus a plot of 20 × 20 m) and the longer sides lie along the contours (to minimize altitudinal effects). It has a ground area in horizontal projection of 0·85 ha. The ground surface is very irregular with limestone boulders protruding for 2–3 m.

The soils are very shallow (average depth 11 cm; range 0–55 cm), highly organic and black with a mull-humus form. They occur as interstitial material between hard, sharply-angled or pointed limestone rocks. Bare rock accounts for 9% of the ground surface.

METHODS

Forest description

The four sites were marked out and sub-divided into twenty-five (20 × 20 m) plots all measured without slope correction and used as a sample grid in subsequent investigations. One sub-plot (5 × 5 m) was selected at random within each of fifteen plots which had been selected in a restricted random way so that they were spread over the site. Each sub-plot was divided into four (2·5 × 2·5 m) quadrats.

The diameters of all trees (≥10 cm dbh) in each of the sites were measured on one occasion between October 1977 and August 1978. The measurements were made at breast height (1·3 m) except for those trees with large buttresses or prop roots which had their diameters measured above these protrusions (usually at a height of about 2 m). A few trees on the LF had multiple stems and each stem was measured separately. Over the same period the height of each tree on the AF, DF and HF was measured using a Haga gauge. Tree heights on the LF were difficult to measure because of the terrain and most of the heights there were estimated from a regression of height on dbh, calculated from thirty-four trees (≥10 cm dbh) for which heights had been measured for the profile diagram (Fig. 5). On all the sites each tree was identified so far as possible. A transect (60 × 7·5 m) of mature-phase forest within each site was selected for a profile diagram of trees over 6 m high.

The smaller plants were not identified but were assessed as follows. Within each sub-plot the stem diameter of all the trees (≥1 m high) was measured; at 1·3 m above ground level for all trees 3 m or more tall and at the mid-point for those less than 3 m. The heights of all these smaller trees were estimated visually. All lianes, including rattans, within each sub-plot were recorded and placed in three diameter classes: < 1 cm, ≥1 cm < 10 cm, and ≥10 cm. From one of the quadrats, selected randomly within each of the sub-plots, all young trees ≥30 cm tall and, separately, those < 30 cm were counted. From the same quadrats all ground herbs and ferns and all epiphytes (≤3 cm from the ground) were collected, oven-dried at 105 °C for about 48 h and weighed. Epiphytes which occurred more than 3 m from the ground, bryophytes and lichens were not included in the enumerations.

Soil sampling and analyses

Soils were sampled in July and August 1978 at one random point within each of the twenty-five plots on each site. On the AF, DF and HF soil samples were taken at two depths: at 0–10 cm (including the deep humus layer where this existed but excluding recognizable plant remains) and 10–30 cm. In the shallow LF soils, only one set of samples were collected and often these were less than 10 cm deep. On the AF, DF and HF the upper samples and all the LF samples were collected by the use of a metal corer (10 × 10 × 10 cm). The 10–30 cm deep samples were collected from the base of the upper sample hole with a 6-cm diameter Dutch auger. The stones and the larger roots were removed from the samples which were then air-dried in the field and stored in plastic bags prior to analysis in the U.K.

Before analysis the samples were lightly ground using a pestle and mortar and sieved through a 2-mm mesh. Weighed sub-samples were oven-dried at 105 °C so that results for analyses carried out on air-dried soils could be expressed on an oven-dry basis. Acidity was measured on a mixture of 10 g of air-dried soil with 25-ml (occasionally 35-ml in the case of samples with very high organic matter) of deionized water. Loss-on-ignition was measured after heating overnight at 400 °C. Exchangeable cations were extracted for about 16 h from 5 g samples by M ammonium acetate solution adjusted to pH 7 and analysed by atomic absorption spectrophotometry. Lanthanum chloride was added as recommended by Allen *et al.* (1974) before analyses of calcium and magnesium. Total phosphorus was determined colorimetrically in nitric acid digests of 1 g samples by a method based on that of Allen (1940). Cation exchange capacity at a buffered pH of 8·1 was measured by the method of Bascomb (1964). Total nitrogen was extracted by digesting 1 g of air-dried soil in 10 ml of concentrated sulphuric acid with a Kjeldahl (copper) catalyst tablet and the ammonia produced was determined by an automated technique described by Dancer (1975). Organic carbon was determined by the titrimetric Schollenberger method (Metson, Blakemore & Rhoades 1979).

RESULTS

Trees

The profile diagrams (Figs 2–5) give an impression of the overall appearance of the forests: the relatively small stature of the AF, the open DF with its huge emergents, the pole-like aspect of the HF, and the steeply sloping LF.

A summary of tree density, basal area and height is given in Table 1. Differences in basal area are more pronounced than those of density. The trees on the DF have about twice the basal area of those on the AF. The diameter-class distribution of stems clearly shows that the largest occur on the DF (Table 2). Only seven trees on the AF exceeded 40 m in height; in comparison, there were thirty-seven on the DF, forty-seven on the HF and an estimated fifteen on the LF which exceeded this height. The DF was the only site with measured individuals taller than 50 m; the tallest of three trees which exceed this height was a 57·5 m specimen of *Shorea ferruginea* Brandis.

Identification to species was achieved for 87% of the individuals on the AF, 85% on the DF, and 95% on the HF and LF. The remaining specimens were sorted into different taxa to enable a species–area curve to be constructed. A few specimens were lost (two from the AF; twenty-four from the DF; six from the HF; and four from the LF) and these may have included some further species. Species–area curves based on the twenty-five

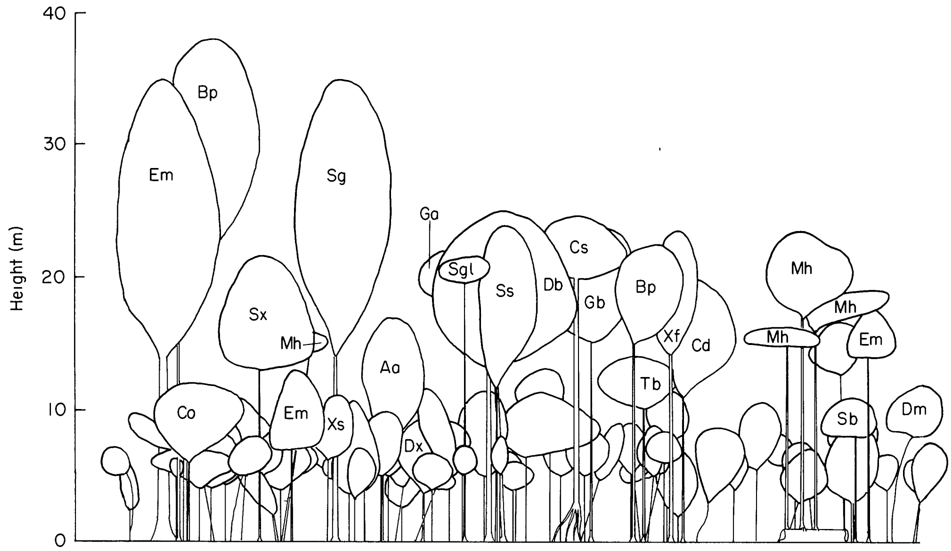

FIG. 2. Profile diagram (60 × 7·5 m) of alluvial forest in Gunung Mulu National Park, Sarawak. Trees less than 6 m high excluded. Symbols for trees over 10 cm dbh: Aa, *Aglaia argentea* Bl.; Bp, *Bhesa paniculata* Arn.; Cd, *Canarium denticulatum* Bl.; Ch, *Chionanthus oliganthus* (Merr.) Kiew; Cs, *Calophyllum sclerophyllum* Vesque; Db, *Diospyros borneensis* Hiern.; Dm, *Dimorphocalyx murinus* Elm.; Dx, *Diospyros* sp.; Em, *Eusideroxylon malagangai* Sym.; Ga, *Goniothalamus andersonii* J. Sinclair; Gb, *Garcinia beccarii* Pierre; Mh, *Macaranga hosei* King ex Hk.f.; Sb, *Sterculia bicolor* Mast.; Sg, *Saurauia glabra* Merr.; Sgl, *Swintonia glauca* Engl.; Ss, *Swintonia specifera* Hk.f.; Sx, *Santiria* sp.; Tb, *Talauma beccarii* Ridl.; Xf, *Xanthophyllum flavescens* Roxb.; Xs, *Xanthophyllum stipitatum* A. W. Bennett.

TABLE 1. The density, basal area, mean basal area and mean height of trees (⩾ 10 cm dbh) and the total above-ground biomass (dry weight) on four sites in Gunung Mulu National Park, Sarawak.

Site	Site area in horizontal projection (ha)	Density (ha^{-1})	Basal area (m^2 ha^{-1})	Mean basal area (m^2 $tree^{-1}$)	Mean height (m)	Total biomass (t ha^{-1})
Alluvial forest	1·00	615	28	0·046	17·8	250
Gley-soil part of alluvial forest	0·40	645	28	0·043	16·3	210
Dipterocarp forest	0·95	778	57	0·073	21·8	650
Heath forest	1·00	708	43	0·061	21·8	470
Forest over limestone	0·85	644	37	0·057	18·8	380

TABLE 2. Percentage of trees (⩾ 10 cm dbh) in a range of diameter-classes in four sites in Gunung Mulu National Park, Sarawak.

Site	Diameter-class (cm) 10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	>100
Alluvial forest	68	17	6·7	4·2	1·3	1·1	+	0·81	+	+
Gley-soil part of alluvial forest	71	16	6·6	3·9	1·6	+	+	0·78	+	0·0
Dipterocarp forest	58	19	10·0	5·7	2·2	2·3	1·8	+	0·81	0·91
Heath forest	62	18	9·8	3·9	1·8	1·4	1·3	1·1	+	0·56
Forest over limestone	66	18	6·1	3·2	2·9	1·4	1·6	+	0·54	+

+, <0·5%.


Height (m)
50
40
30
20
10
0
Sf
Dbe
Hw
Sq
Po
Dbe
Eo
?
Ef
Sp
Mw
Sy
Hw
Sd
Gc
Dbe
Pw
Ec
Dy
Cc
Mc
Df
Ai
Bx
Gp
Ex
Gf
?
Pu
?
Pr
Gk
Dz
Ep
Ep
Ao

FIG. 3.


Height (m)
50
40
30
20
10
0
Sa
Tc
Sm
Ct
Pc
Ct
Ct
Hc
Bb
Lx
Lr
Ct
Dxa
Mc
Pc
Ct
Pg
Lr
Lr
Cb
Hp
Mc
Mc
Gpe
Sc
En
Cb
Cb
Cdi
Kk
Bp
Ct
El
Mc
Cf
Pg
Cha
Mc
Bb
Lp
Ta
Hp

FIG. 4.

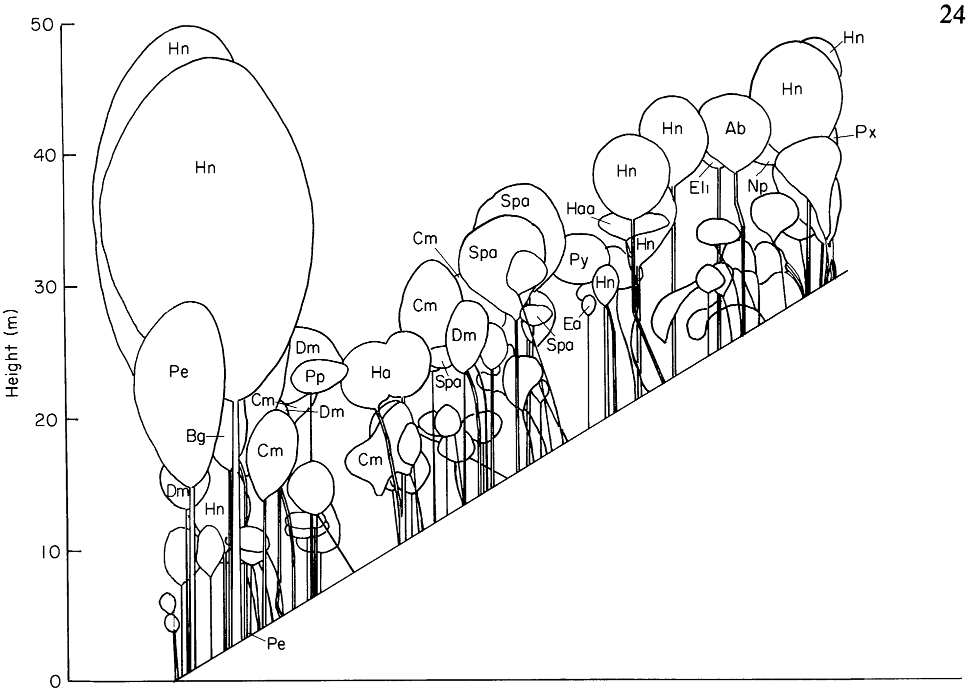

FIG. 5. Profile diagram of forest over limestone in Gunung Mulu National Park, Sarawak. Details as for Fig. 2. Symbols: Ab, *Aglaia bernardoi* Merr.; Bg, *Brownlowia* c.f. *glabrata* Ridl.; Cm, *Cleistanthus myrianthus* (Hassk.) Kurz; Dm, *Drypetes microphylla* (Bl.) P. et H.; Ea, *Eugenia* c.f. *arcuatinervia* Merr.; Eli, *Eugenia lineata* (Bl.) Duthie; Ha, *Harpullia arborea* (Bl.) Radlk.; Haa, *Hopea argentea* W. Meyer; Hn, *Hopea nutans* Ridley; Np, *Nauclea peduncularis* G. Don; Pe, *Palaquium elegans* K. Griffioen et H. J. Lam; Pp, *Pometia pinnata* Forst.; Px, *Planchonella* sp.; Py, *Polyalthia* sp.; Spa, *Shorea patoiensis* Ashton.

FIG. 3. Profile diagram of dipterocarp forest in Gunung Mulu National Park, Sarawak. Details as for Fig. 2. Symbols: Ai, *Aporusa illustris* Airy Shaw; Ao, *Artocarpus odoratissimus* Blanco; Bx, *Buchanania* sp.; Cc, *Canarium caudatum* King f. *caudatum*; Dbe, *Dryobalanops beccarii* Dyer; Df, *Dehaasia firma* Bl.; Dy, *Dacryodes* sp.; Dz, *Diospyros* sp.; Ec, *Eugenia castanea* Merr.; Ef, *Elaeocarpus floribundus* Bl.; Eo, *Eugenia ochneocarpa* Miq.; Ep, *Eugenia prasiniflora* Ridl.; Ex, *Eugenia* sp.; Gc, *Gymnacranthera contracta* Warb.; Gf, *Gonystylus forbesii* Gilg.; Gk, *Ganua* c.f. *kingiana* (Brace) V.d. Assem.; Gp, *Ganua prolixa* Dub.; Hw, *Hydnocarpus woodii* Merr.; Mc, *Myristica cinnamomei* King; Mw, *Melanorrhoea wallichii* Hk.f.; Po, *Payena* c.f. *obscura* Burck.; Pr, *Palaquium ridleyi* King et Gamble; Pu, *Parastemon urophyllum* D.C.; Pw, *Palaquium walsurifolium* Pierre ex Dubard; Sd, *Sarcotheca diversifolia* (Miq.) Hall. f.; Sf, *Shorea ferruginea* Brandis; Sp, *Shorea parvistipulata* Heim; Sq, *Shorea quadrinervis* V.Sl.; Sy, *Santiria* sp.; ?, unidentified species.

FIG. 4. Profile diagram of heath forest in Gunung Mulu National Park, Sarawak. Details as for Fig. 2. Symbols: Bb, *Baccaurea bracteata* Muell.-Arg.; Bp, *Bhesa paniculata* Arn.; Cb, *Cephalomappa beccariana* Baill.; Cdi, *Canthium didymum* (Bedd.) Gaertn.f.; Cf, *Castanopsis foxworthyi* Schottky ex Winkler; Cha, *Calophyllum havilandii* Ind.; Ct, *Calophyllum teijsmannii* Miq.v. *teijsmannii*; Dxa, *Diospyros* sp.; El, *Eugenia leucoxylon* Miq.; En, *Eugenia nemestrina* Hend.; Gpe, *Garcinia* c.f. *petiolaris* Pierre; Hc, *Horsfieldia crassifolia* (Hk.f. et Th.); Hp, *Hopea pentanervia* Sym. ex Wood; Kk, *Knema kunstleri* (King) Warb. v. *kunstleri*; Lp, *Lithocarpus pseudokunstleri* A. Camus; Lr, *Lophopetalum rigidum* Ridl.; Lx, *Lithocarpus* sp.; Mc, *Mesua calophylloides* (Ridl.) Kosterm.; Pc, *Palaquium cochleariifolium* Van Royen; Pg, *Polyalthia glauca* (Hassk.) Boerl.; Sa, *Shorea albida* Sym.; Sc, *Sindora coriacea* Maing. ex Prain.; Sm, *Stemonurus malaccensis* (Mast.) Sleumer; Ta, *Ternstroemia aneura* Miq.; Tc, *Tristania clementis* Merr.

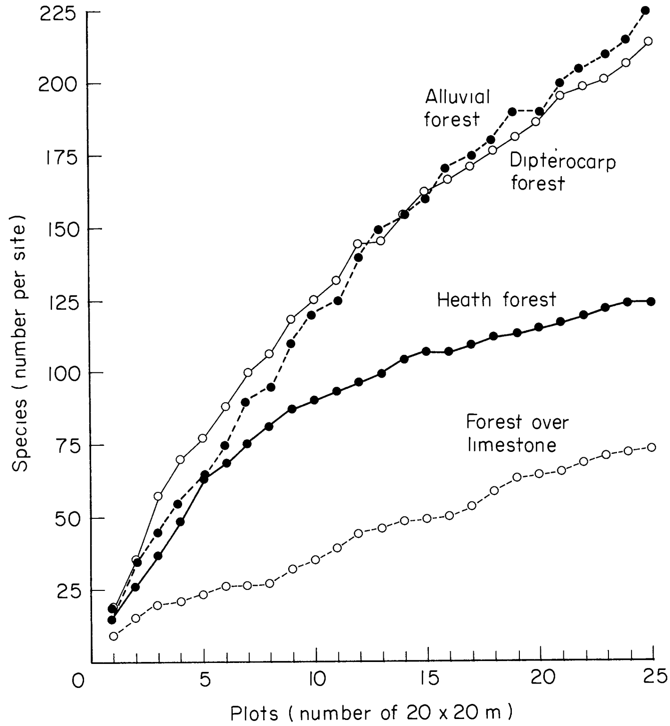

FIG. 6. Species–area curves for trees (⩾10 cm dbh) on the four sites in Gunung Mulu National Park, Sarawak. Each curve follows the order of enumeration of the twenty-five plots. Symbols: ●----●, AF; ○——○, DF; ●——●, HF; ○---○, LF. (On the AF, plots 1–10 were GAF).

contiguous plots on each site are shown in Fig. 6. None of the curves have reached the asymptote although it is most closely approached on the HF and LF.

Table 3 indicates that the Dipterocarpaceae are the most important family in terms of both basal area and numbers of trees on the DF and LF. This family has the highest basal area on the HF, but is second to the Guttiferae in numbers of individuals. On the AF the Dipterocarpaceae are relatively less important, being second after the Leguminosae in basal area and the sixth family in numbers of individuals. The minor contribution of the Dipterocarpaceae in the GAF is noteworthy. By contrast, trees of the Ebenaceae, Meliaceae, Sapindaceae and Sterculiaceae on the AF have at least 70% of their individuals on the GAF.

Smaller plants

A comparison of the sites is given in Table 4 for small trees, in Table 5 for lianes, and in Table 6 for ground herbs and epiphytes. There are large differences between the sites in these small components of the vegetation.

Biomass estimation

A number of empirically validated regressions, e.g. Anon. (1978) and Kira (1978) have been used to estimate trunk, branch, and (by their addition) total woody biomass. These regressions are not likely to be of general application because of the great variations

TABLE 3. The percentage contribution of the ten most abundant families on each site to tree (⩾10 cm) basal area (B.A.) and the actual numbers of individuals in each of these families on four study sites in Gunung Mulu National Park, Sarawak. (The ten highest values in each column are printed in italics.)

	Alluvial forest		Gley-soil part of alluvial forest		Dipterocarp forest		Heath forest		Forest over limestone	
	B.A.%	No.	B.A.%	No.	B.A.%	No.	B.A.%	No.	B.A.%	No.
Abundant on all sites										
Dipterocarpaceae	*13·0*	*33*	*11·5*	*8*	*43·2*	*114*	*42·9*	*92*	*47·4*	*140*
Euphorbiaceae	*8·9*	*97*	*10·8*	*42*	*2·8*	*70*	*3·0*	*65*	*5·8*	*89*
Myrtaceae	*6·4*	*44*	*4·5*	*15*	*4·0*	*65*	*11·0*	*74*	*5·1*	*47*
Sapotaceae	*4·8*	*30*	0·9	4	*4·8*	*52*	*3·3*	*38*	*4·1*	*39*
Present on all sites										
Anacardiaceae	*4·2*	12	*4·0*	6	1·5	*20*	*2·1*	12	0·1	1
Annonaceae	2·0	18	1·3	5	0·5	4	*2·6*	*32*	0·7	9
Burseraceae	0·8	13	1·0	4	*3·1*	*35*	0·3	3	0·3	2
Ebenaceae	*4·7*	*37*	*10·5*	*30*	0·3	8	0·5	7	1·0	*16*
Guttiferae	*5·2*	*42*	*5·4*	*19*	*2·2*	*35*	*17·0*	*170*	0·7	7
Lauraceae	*5·5*	*28*	*8·6*	*14*	*2·6*	*20*	1·5	8	*1·8*	*13*
Leguminosae	*15·1*	*43*	*23·6*	*25*	*5·1*	*15*	1·7	*18*	0·2	4
Meliaceae	2·1	*23*	*4·2*	*20*	0·0	1	0·1	3	*3·6*	*50*
Myristicaceae	2·7	*29*	1·9	4	*2·4*	*49*	1·1	*25*	0·3	4
Sapindaceae	1·3	10	*2·5*	*7*	0·6	8	0·2	2	*9·5*	*25*
Sterculiaceae	2·7	10	*6·4*	*9*	0·4	4	0·1	2	*3·3*	*14*
Absent from forest over limestone										
Celastraceae	1·2	8	1·2	4	1·6	*15*	*1·8*	*43*	—	—
Fagaceae	1·7	11	2·0	3	*2·6*	*15*	0·9	*21*	—	—
Thymelaeaceae	0·8	3	0·2	1	0·3	6	*2·9*	16	—	—
In forest over limestone only										
Combretaceae	—	—	—	—	—	—	—	—	*1·5*	7
Absent from heath forest and forest over limestone										
Bombacaceae	*2·9*	3	—	—	0·1	1	—	—	—	—
Absent from alluvial and dipterocarp forests										
Crypterionaceae	—	—	—	—	—	—	*1·8*	5	0·0	1
Absent from heath forest										
Tiliaceae	0·2	2	0·2	1	0·3	4	—	—	*7·8*	*32*

between stem and crown proportions according to age and stand-density (Gray 1956, 1966; H. C. Dawkins, personal communication). There is much less variation if total above-ground volume is measured. It has been shown (Dawkins 1961, 1963) that for trees of many species and a wide range of sizes the above-ground wood and bark volume can be calculated as: height × basal area × 0·5. The calculated value is a theoretically sound figure which agrees with the quadratic paraboloid theory of tree form (H. C. Dawkins, personal communication). The specific gravity of fresh wood and of bark varies greatly

TABLE 4. The estimated basal areas (m^2 ha^{-1}) of small trees (⩾ 1 m high and < 10 cm dbh) and the density (m^{-2}) of small trees (⩾ 0·3 m–< 1 m high, and < 0·3 m high) on four sites in Gunung Mulu National Park, Sarawak. Mean values and 95% confidence limits are given.

Site	Basal area (m^2 ha^{-1})	Density of trees (⩾ 0·3 m–< 1 m high) (m^{-2})	Density of trees (< 0·3 m high) (m^{-2})
Alluvial forest	8·3 ± 1·9	2·2 ± 0·6	3·2 ± 1·1
Gley-soil part of alluvial forest	7·4 ± 2·2	1·8 ± 0·7	1·9 ± 0·6
Dipterocarp forest	4·8 ± 1·4	2·1 ± 1·1	3·7 ± 0·8
Heath forest	7·9 ± 2·3	2·0 ± 0·7	4·1 ± 1·1
Forest over limestone	5·1 ± 1·3	4·8 ± 1·8	6·9 ± 1·8

TABLE 5. Estimated density (ha^{-1}) of lianes (including rattans) of three size-classes on four sites in Gunung Mulu National Park, Sarawak. Mean values ± 95% confidence limits are given.

Site	Diameter-class (cm) < 1	1–10	> 10
Alluvial forest	14 400 ± 3360	1960 ± 640	292 ± 284
Gley-soil part of alluvial forest	13 000 ± 4800	4800 ± 5200	332 ± 680
Dipterocarp forest	2160 ± 800	440 ± 260	0
Heath forest	2040 ± 880	440 ± 324	0
Forest over limestone	10 700 ± 3920	4040 ± 1080	32 ± 67

TABLE 6. Estimated oven-dry weight (kg ha^{-1}) (± 95% confidence limits) of ground herbs and epiphytic vascular plants which grow within 3 m of the ground on four sites in Gunung Mulu National Park, Sarawak.

Site	Ground herbs	Epiphytes
Alluvial forest	257 ± 312	45·4 ± 23·0
Gley-soil part of alluvial forest	574 ± 866	45·6 ± 30·3
Dipterocarp forest	10·8 ± 10·4	0·26 ± 0·47
Heath forest	26·9 ± 39	86·6 ± 49·4
Forest over limestone	11·1 ± 8·2	2·9 ± 3·6

with species but there is evidence that in mature species-rich rain forest it averages 0·6 g cm^{-3} (Odum 1970; Huttel & Bernhard-Reversat 1975). Edwards & Grubb (1977) have suggested that, by multiplying the large woody biomass (calculated for trees ⩾ 7 cm dbh using the above formula) by a factor of 1·1–1·2, a value for total above-ground biomass (including leaves, small twigs, epiphytes, lianes and other life forms) is obtained. This factor is based on very few data and since our sites vary greatly in their numbers of smaller plants (Tables 4–6) its use here is questionable. However, we have multiplied the biomass values for trees (⩾7 cm dbh) by 1·1 to give a rough estimate of total above-ground biomass (Table 1).

The site biomass estimates (Table 1) are in the order DF > HF > LF > AF > GAF. Edwards & Grubb (1977) suggested that the minimal area principle could be used to test if the site biomass was representative of larger areas of forest and that successive plots should be sampled until the cumulative mean changes by less than 10%. This criterion is met for the trees (⩾10 cm dbh), which form the greater part of the biomass, on the plots (Fig. 7).

However, our sites cannot be regarded as certainly representative of their forest types. First, 1 ha is not a large area in forest with big trees. Secondly, we know little of the pattern of variation of biomass; Edwards & Grubb (1977) have pointed out that there may be patches of different scales, e.g. 0·1 ha, 1·0 ha and 10 ha. Thirdly, the graphs in Fig. 6 show a substantial slope for the last nineteen points for the DF and the last nine points for the LF.

The marked drop from the first to the second point in each curve in Fig. 6 was surprising. We explain it as a subconscious bias in the initial selection of the sites. The first corner (which would delimit the first 20 × 20 m plot in Fig. 7) invariably included large trees and no gaps. The order of the plots in Fig. 7 is that in which they were enumerated in the field. Clearly the shape of the graphs in Fig. 7 depends on the order of the plots and, since other sequences are as logical as the ones chosen, this is an additional problem in interpreting running-mean biomass curves.

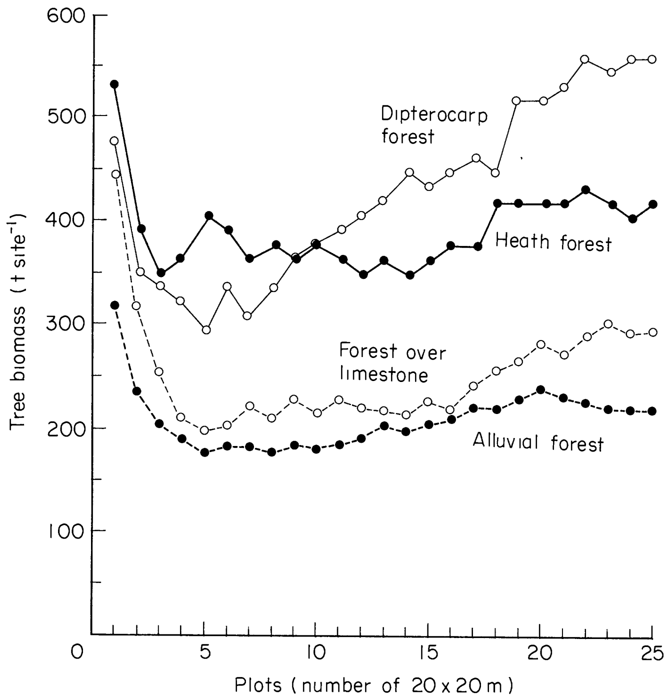

FIG. 7. The running-mean above-ground dry weight estimates for trees (⩾10 cm dbh) in increasing numbers of plots (following the order of their enumeration) on the four sites in Gunung Mulu National Park, Sarawak. Symbols: ●----●, AF; ○——○, DF; ●——●, HF; ○----○, LF. (On the AF, plots 1–10 were GAF).

Soil analysis

Tests showed that in nearly all cases the analytical data were not normally distributed and they will be discussed in more detail in a later paper. The mean values are given in Table 7 and from these the following major points emerge.

(i) The pH values for the HF are the lowest with a mean of 3·6 in the 0–10 cm samples. The corresponding value for the DF is 4·1. Low values occurred in the podzolic soils of the highest parts of the AF, but in the GAF (and also in all samples from the LF) pH was much higher but all were less than pH 7·2.

(ii) The concentration of total exchangeable bases (K, Na, Ca and Mg) was least on the DF soils and samples from this site have particularly low concentrations of calcium and a high proportion of potassium in comparison with other sites. The AF soil is base rich because of flooding by the Melinau River. The LF receives a high base supply from weathering bedrock judging from the dominance of Ca^{++}. The percentage base saturations are ranked in the order GAF > LF > AF > HF > DF.

(iii) Total nitrogen concentration was highest on the LF site and least on the DF. The HF soils had a relatively high total nitrogen concentration but we have no data on rates of mineralization. Total phosphorus concentration was highest in the LF soil and least in some samples from the DF and HF. However, we have no measurement of potentially available phosphorus.

(iv) Most of the soils from all sites had relatively high values for organic carbon and there were many significant correlations involving soil organic carbon (which is

TABLE 7. Means of soil pH; percentage loss-on-ignition; concentrations of organic carbon, total nitrogen, total phosphorus and exchangeable potassium, sodium, calcium and magnesium; C/N quotients; cation exchange capacity, and percentage base saturation, in samples from four tropical forests in Gunung Mulu National Park, Sarawak.

Site	Sample depth (cm)	*n*	pH	Loss-on-ignition* (%)	C* (%)	N* (%)	C/N†	P* ($\mu g\ g^{-1}$)	K*‡	Na*‡	Ca*‡	Mg*‡	C.E.C.*‡	Base saturation† (%)
Alluvial forest	0–10	24	4·4	20	12	0·54	28	270	0·24	0·082	5·3	0·53	38	30
	10–30	24	4·8	6·5	3·4	0·26	19	140	0·053	0·045	2·5	0·14	15	23
Gley-soil type within alluvial forest	0–10	10	5·2	13	7·7	0·54	14	340	0·16	0·069	11·3	0·66	20	59
	10–30	10	5·4	5·0	2·9	0·20	15	210	0·045	0·051	5·7	0·22	11	51
Dipterocarp forest	0–10	25	4·1	19	11	0·51	33	120	0·25	0·059	0·039	0·18	37	1·6
	10–30	25	4·7	5·1	2·1	0·15	15	140	0·047	0·035	0·018	0·039	12	1·3
Heath forest	0–10	25	3·6	54	29	0·91	33	280	0·54	0·11	0·67	1·5	110	2·9
	10–30	25	4·0	15	9·2	0·36	36	74	0·082	0·025	0·075	0·16	31	1·5
Forest over limestone	0–$\leqslant$10	25	6·1	82	42	2·5	17	560	0·58	0·15	61	6·1	210	32

* Values are expressed per weight of oven-dry (105 °C) soil.
† Values are the means of C/N quotients or percentage base saturations of individual samples.
‡ Units are m-equiv. per 100 g soil.

TABLE 8. Correlation coefficients (r_s) between percentage organic carbon and concentration of total nitrogen, and total phosphorus, exchangeable bases, and cation-exchange capacity (C.E.C.), in soil samples from four tropical forest sites in Gunung Mulu National Park, Sarawak. All values are significant with $P < 0{\cdot}01$ except those marked *, where $P < 0{\cdot}05$; and †, which are not significant.

Site	Sample depth (cm)	*n*	N	P	Ca	Mg	K	Na	C.E.C.
Alluvial forest	0–10	24	0·881	0·693	−0·068†	0·772	0·875	0·873	0·962
	10–30	24	0·679	0·513	0·468*	0·583	0·589	0·579	0·674
Dipterocarp forest	0–10	25	0·734	0·009†	0·426*	0·834	0·921	0·732	0·926
	10–30	25	0·788	0·358*	0·311†	0·716	0·512	0·245†	0·612
Heath forest	0–10	25	0·911	0·734	0·574	0·775	0·774	0·704	0·871
	10–30	25	0·704	0·722	0·607	0·758	0·807	0·469*	0·888
Forest over limestone	⩽10	25	−0·026†	−0·242†	0·088†	0·176†	0·027†	0·110†	0·337*

accepted as a good measure of soil organic matter) and concentration of exchangeable bases, cation exchange capacity, and total nitrogen and phosphorus (Table 8). Soil organic matter contains the principal cation exchange sites in acid tropical soils (Sanchez 1976) and is generally recognized as a major pool of biologically circulating phosphorus in the soil and the main pool of soil nitrogen. The low level of correlation with exchangeable calcium on the AF can be explained in terms of the inundation by calcareous water of the gley soils of low organic matter content. The lack of significant correlations in some cases for the DF soils may be due to the higher clay content of the soil (Tie *et al.* 1979) which makes an important contribution to the soil nutrient pool. The LF soils showed no significant correlations except with cation exchange capacity. This is not surprising since the organic matter, which is consistently high in the LF, might be expected to show a number of unrelated differences in chemical composition between samples.

(v) Differences in organic matter content between samples imply that there are large differences between soils in bulk density and that soil analyses expressed on a weight basis may be misleading. To assess this the bulk density of each soil sample was calculated from the percentage soil loss-on-ignition using the equation of Jeffrey (1970). The use of this equation seems reasonable since on all the four sites and at all sample depths there was a close linear relationship between the chemically determined soil organic carbon and percentage loss-on-ignition. Even in the most clay-rich samples the soil organic carbon was only occasionally substantially less than half the loss-on-ignition value. Some analytical results from Table 7 are expressed on an area–depth basis in Table 9 which should be

TABLE 9. Estimated weights of exchangeable bases and total nitrogen, phosphorus, and organic carbon in (the top 30 cm of) soils from the alluvial, dipterocarp and heath forest sites and (in the top 11 cm of soil) from the forest over limestone site in Gunung Mulu National Park, Sarawak. The weights are estimated from data in Table 7 and soil bulk-density values calculated from percentage loss-on-ignition from the regression of Jeffrey (1970).

Site	C ($t\ ha^{-1}$)	N ($kg\ ha^{-1}$)	P ($kg\ ha^{-1}$)	K ($kg\ ha^{-1}$)	Ca ($kg\ ha^{-1}$)	Mg ($kg\ ha^{-1}$)	Na ($kg\ ha^{-1}$)
Alluvial forest	120	7800	420	95	1600	69	30
Dipterocarp forest	99	6000	360	96	4·6	22	24
Heath forest	160	7800	190	50	62	82	16
Forest over limestone	82	5000	120	46	2400	150	6·8

interpreted as a rough guide only. Compared with Table 7, the most important differences are the relatively lower values in general for the LF and for exchangeable potassium and total phosphorus in the HF.

It was not possible to take into account the differences in rooting depth. I. C. Baillie (personal communication) has shown the presence of roots down to 1·5 m on the DF. It may be that the values in Table 9 to some extent underestimate plant-available nutrients on the DF soil. However, the evidence from element concentrations in litterfall (Proctor *et al.* 1983) confirms the view that nutrients are likely to be in short supply in the DF soil.

DISCUSSION

Forest structure, physiognomy and floristics

Dawkins (1958, 1959) estimated that the pantropical average basal area of most virgin lowland rain forests is about 36 $m^2\ ha^{-1}$ for trees > 30 cm girth. This value is exceeded on both the HF and DF. The basal area of the HF trees is above the mean of 37 $m^2\ ha^{-1}$ for trees (> 3·1 cm gbh) for all heath forests investigated by Brünig (1974) but within his computed range for heath forests of 17–88 $m^2\ ha^{-1}$. The HF is at the taller end of the range described by Brünig.

The biomass estimates for the four sites described in this paper can be compared with those summarized by Edwards & Grubb (1977) for lowland rain forests and semi-deciduous forests. These range from 233 t ha^{-1} for secondary forest in Ghana to 475 t ha^{-1} for primary forest in Malaya. The total above-ground biomass of a lowland rain forest plot at Pasoh in Peninsular Malaysia was estimated at 431 t ha^{-1} (Kira 1978). Our biomass estimates extend from the lower range, from 250 t ha^{-1} for the AF (GAF 210 t ha^{-1}) to the DF, which at 650 t ha^{-1}, is clearly very high. Some of the DF is on sloping ground and this accounts partly for the very high value. Considerably larger values exist for forests in Borneo (e.g. Ashton 1964) but these remain to be quantified.

It is often assumed that forest biomass is related to soil nutrient status but our studies show no clear relationship between the measured soil nutrients and forest structure. It is noteworthy that, despite its huge biomass, the DF has soils that have very low concentrations of calcium, phosphorus and magnesium whilst the soils under the small-stature GAF have comparatively high concentrations of plant nutrients. Many factors, including different patterns of regeneration, might influence forest biomass. An occasionally flooded forest, such as the GAF, might be expected to have rather shallow roots, frequent tree fall and low biomass. A proportional relationship between soil nutrient concentration and forest biomass would be more likely in young secondary forests (as long as other factors are not limiting) than in undisturbed primary forests with efficient nutrient cycling and long-term nutrient accumulation in living matter from the soil and rain water.

The AF and DF are extremely rich in tree (⩾10 cm dbh) species. The HF is less species-rich than the AF and DF but more so than many rain forests elsewhere which do not have heath forest characteristics. The LF is the least species-rich—a surprising result in view of statements by Anderson (1965) for Sarawak and Chin (1977) for peninsular Malaysia who reported extremely rich limestone floras. Their conclusions apparently do not apply to trees (⩾10 cm dbh) growing on the lower slopes of hills.

Hall & Swaine (1976) found, for a number of Ghanaian forests (under rainfalls that are in the critical range for forest development) that species richness was inversely related to total exchangeable bases. Huston (1980) demonstrated a negative correlation between available soil nutrients (except magnesium, manganese and nitrogen) and species richness in Costa Rican forests. It is intriguing that in our study the LF is most species poor and occurs on nutrient-rich soils whilst the DF is very species rich and occurs on nutrient-poor soils. The gley soils of the GAF are very species rich however and high in nutrients. It seems probable that species richness depends on many factors which may interact and be limiting in different situations so that simple interpretations involving single factors are usually impossible.

The DF had some unusual floristic features: there are some distinctive tree species from the heath forest–dipterocarp forest ecotone (P. S. Ashton, personal communication) and a number of palms characteristic of heath forest (e.g. *Areca minuta* Scheff.; *Calamus ashtonii* Dransf. nov. sp.; *Daemonorops formicaria* Becc.; *Pinanga tomentella* Becc. and *Pogonotium divaricatum* Dransf.) (J. Dransfield, personal communication). These features of the DF are discussed in the next section in relation to the soil analyses.

Comparisons of soil analyses

Table 10 includes data from a number of lowland tropical soils developed from different parent materials and under different climates and which support rain forest. Comparisons of cation exchange capacity (and percentage base saturation) must be made with caution since they depend on the pH at which it is determined (Sanchez 1976). The heath forest soil analyses of Andriesse (1971) are from a site with a higher percentage base saturation and lower cation exchange capacity than the HF. The most striking difference is the relatively high magnesium in the HF samples and it is regrettable that Andriesse gives no details of the vegetation overlying his soils. Andriesse (1969) reported an analysis from a Sarawak heath forest on a podzol developed on Pleistocene deposits (as the Mulu example) which shows a much higher concentration of magnesium and contrasts with his analysis reported in Table 10 which is from a podzol developed on quartzitic sandstone. Considerable variations occur within Sarawak podzols bearing heath forest.

The DF soils are similar to those of the Nyalau series (Andriesse 1971) in having low calcium and a preponderance of potassium amongst the exchangeable cations. The soils collected by Collins (unpublished) from Sawai are of interest since this site possesses some of the best dipterocarp forest in Sarawak. In the Sawai samples, percentage base saturation, exchangeable calcium and magnesium and total phosphorus are higher than in those from the DF whilst percentage organic carbon, C/N quotient, exchangeable sodium and potassium are lower. Most of these differences from the DF samples are shown to a lesser extent by samples from a local dipterocarp forest type within Gunung Mulu National Park (J. Proctor, J. M. Anderson & H. W. Vallack, unpublished). P. S. Ashton (personal communication) pointed out that this local dipterocarp forest lacked a heath forest element in its flora. It is tempting to regard the low calcium and phosphorus concentrations in the soil of the DF as limiting breakdown of soil organic matter and causing the distinctive features of the vegetation. Both Ashton (1973) and Baillie (1978) have regarded phosphorus as an influential determinant of floristic variation in dipterocarp forest. However, in the Park there are examples of soils with high calcium and phosphorus concentrations (on the LF) yet with very high concentrations of organic matter and low rates of decomposition (Anderson, Proctor & Vallack 1983). The accumulation of soil organic matter is a complex and little understood process in tropical forests (Anderson, Proctor & Vallack 1983). Furthermore the plants characteristic of heath forest on the DF are difficult to explain since the soils on the HF are different in important ways from those of the DF. These differences between soils under the same forest formations in Sarawak

TABLE 10. Soil analyses from the upper 30 cm of a range of lowland tropical rain forests.

Forest type and location	Soil series or type	Sample depth (cm)	*n*	pH	C (%)	Exchange bases and cation exchange capacity (C.E.C.) (m-equiv 100 g^{-1}) Ca	Mg	Na	K	C.E.C.	Total N (%)	Total P ($\mu g\ g^{-1}$)	Reference
Dipterocarp; Pasoh, Malaysia	Durian series	0–2	n.d.	4·5	2·7	1·7	0·91	0·09	0·17	8·1	0·27	290	Allbrook (1973)
		2–20	n.d.	4·3	0·5	0·28	0·10	0·08	0·58	5·6	0·17	200	
Dipterocarp; Pasoh, Malaysia	Munchong series	0–1	n.d.	4·3	2·6	0·55	0·47	0·11	0·51	7·5	0·27	200	
		1–25	n.d.	4·4	0·3	0·25	0·07	0·09	0·10	2·5	0·04	100	
Dipterocarp; Sarawak	Nyalau series	0–5	n.d.	3·8	3·6	0	0	0	0·14	15	0·21	n.d.	Andriesse (1971)
		5–17	n.d.	4·8	2·1	0	0	0	0·09	11	0·14	n.d.	
Heath forest; Sarawak	Silantek series	0–5	n.d.	3·0	26	0·54	0·02	0·40	0·25	15	1·0	n.d.	
		5–13	n.d.	3·3	4·8	0·42	0·02	0·39	0·17	6·4	0·16	n.d.	
		13–23	n.d.	4·2	0·46	0·30	0·01	0·33	0·05	3·0	0·02	n.d.	
Dipterocarp; Andalau, hill sites, Sarawak	n.d.	0–1	2	3·8	1·9	0·20	n.d.	n.d.	0·20	n.d.	0·51	55	Ashton (1964)
		within 1–30	5	4·4	1·5	0·16	n.d.	n.d.	0·19	n.d.	0·51	130	
Dipterocarp; Andalau, valley sites, Sarawak	n.d.	within 15–20	4	4·2	11	0·19	n.d.	n.d.	0·54	n.d.	0·43	190	
Dipterocarp; Belalong, Sarawak	n.d.	13	6	4·4	4·1	0·14	n.d.	n.d.	0·21	n.d.	0·29	240	
Undisturbed rain forest; 'site 1', north-eastern Australia	n.d.	0–10	5	6·6	5·4	29	4·6	0·06	1·1	43	0·59	3500	Brasell, Unwin & Stocker (1980)
		10–20	5	6·4	3·6	21	3·2	0·06	0·65	37	0·45	3300	
		20–30	5	6·1	2·2	14	2·7	0·05	0·46	31	0·29	3000	
Undisturbed rain forest; 'site 2' north-eastern Australia	n.d.	0–10	5	5·1	5·0	5·2	2·9	0·11	0·32	28	0·49	2400	
		10–20	5	4·9	3·3	2·2	1·5	0·08	0·17	21	0·38	2300	
		20–30	5	4·8	2·1	0·8	0·7	0·05	0·09	18	0·25	2200	
Dipterocarp; Sawai, Sarawak	n.d.	0–20	20	4·4	1·9	0·12	0·35	0·02	0·09	9·8	0·17	170	N. M. Collins (unpublished)
Mature secondary semi-deciduous forest; Kade, Ghana	n.d.	0–5	24	5·3	2·3	5·5	1·1	n.d.	0·46	9·2	0·20	n.d.	Greenland & Kowal (1960)
		5–30	24	4·7	0·74	2·3	0·59	n.d.	0·33	6·1	0·10	n.d.	
Caatinga forest; San Carlos, Venezuela	spodosol	0–8	n.d.	3·8	8·2	2·4	0·32	0·14	0·57	n.d.	0·12	n.d.	Herrera (1979)
		8–23	n.d.	4·1	4·6	0·57	0·18	0·097	0·12	n.d.	0·16	n.d.	
Peru	Rich soils with lush vegetation	0–4	5–10	6·1	13*	4·5	0·65	0·070	0·87	32	0·32	n.d.	Stark (1971)
		20–22	5–10	5·9	5·3*	1·3	0·28	0·078	0·34	21	0·24	n.d.	
Forests (terra firme); Brazil	spodosol A	0–4	n.d.	4·4	7·4*	0·055	0·025	0·087	0·074	9·4	0·12	n.d.	
		20–22	n.d.	4·0	3·6*	0·025	0·025	n.d.	0·031	6·8	0·066	n.d.	
	spodosol B (A has better forest than B)	0–4	n.d.	4·1	8·7*	0·060	0·082	0·048	0·17	26	0·16	n.d.	
		20–22	n.d.	4·2	2·1*	0·13	0·090	0·052	0·16	7·6	0·061	n.d.	
'Igapo' fluvial forest; Brazil	n.d.	0–4	n.d.	4·0	14*	0·095	0·21	0·022	0·36	22	0·72	n.d.	
		20–22	n.d.	4·2	n.d.	0·33	0·041	0·065	0·092	24	0·055	n.d.	
Forest (on terra firme); Rio Negro, Branco, Brazil	spodosol	0–4	n.d.	4·2	12*	0·055	0·30	0·22	1·0	13	0·87	n.d.	
		20–22	n.d.	4·2	7·7*	0·035	0·049	0·57	1·6	10	0·41	n.d.	
'Capoeira' (second growth) forest; Rio Negro, Brazil	spodosol	0–4	n.d.	4·3	n.d.	0·14	0·033	0·070	0·12	7·0	0·080	n.d.	
		20–22	n.d.	4·1	n.d.	0·15	0·049	0·043	0·061	9·2	0·062	n.d.	

* Calculated as 0·5 × loss-on-ignition %.
n.d., no data.

probably result from differences in parent material and emphasize the need to consider the geological and geomorphological factors in order to understand rain forest soils.

The analyses for the DF and HF show soils as low in nutrients as those from Amazonian forests reported by Stark (1971) and Herrera (1979). Analyses of a large number of soils (Camargo & Falesi 1975) from the Central Plateau and Transamazonic Highway regions of Brazil show base saturation ranging from 5% to 92% and pH from 3·8 to 7·2. Soil analyses from Colombia (Guerrero 1975) show base saturation from 1% to 94% and pH from 4·0 to 5·7. Relatively few of these tropical American soils have as low a pH or percentage base status as those from the HF and DF. At the other end of the spectrum, the analyses by Brasell, Unwin & Stocker (1980) from Australia and Greenland & Kowal (1960) from Ghana show base-rich soils under tropical rain forests. Although some differences (particularly of cation exchange capacity) will be exaggerated by differences in analytical methods the wide ranges in Table 10 are very striking and warn against generalizations about tropical forest soils.

Leaves on the heath forest site

Heath forest tree leaves are typically hard, glossy, scleromorphic notophylls and microphylls. Drought and low soil nutrients have been suggested (Brünig 1974) as the causes of these features.

It is difficult to believe that drought is a prime cause since the heath forest site graded into 'kerapah' forest on water-logged soils where species with similar leaves to those in the heath forest seemed well represented. Moreover the LF (which is about 2 km distant from the HF and almost certainly experiences the same climate) is developed on shallow soils yet the trees have softer mesophylls. Recent experiments (Peace & Macdonald 1981) on the rate of water loss of cut shoots and on the sub-lethal water deficit of detached leaves of eight heath forest tree species (from Bako National Park, Sarawak) showed values all within the range recorded for lowland rain forest species. It was concluded that the species studied had no special ability to avoid or resist desiccation.

The soil chemical analyses expressed on a volume basis (Table 9) suggest that heath forest soils may be deficient in potassium and phosphorus but not in nitrogen. However, these results are probably not a good guide to plant-available quantities of these elements. Proctor *et al.* (1983) found that a low nitrogen concentration is the most distinctive nutrient element feature of litterfall in the HF and it seems likely that this factor determines some of its leaf characteristics. It might be argued that since scleromorphic leaves generally have a high C/N quotient then this would cause low concentrations of nitrogen in litterfall even if these leaves were an adaptation to some other factor. However it is noteworthy that the small wood litterfall as well as the leaf litterfall has a relatively low nitrogen concentration suggesting that low nitrogen is a pervading character of heath forest. It is relevant that some heath forest features, including the presence of pitcher plants, occur in upper montane forests on Gunung Mulu and these also have litterfall which has relatively a low concentration of nitrogen (J. Proctor, J. M. Anderson & H. W. Vallack, unpublished). The distinctively low pH (Table 7) of the highly organic heath forest surface soils may limit the mineralization of the organic nitrogen. The low pH may result from a lack of aluminium-containing minerals since aluminium ions positively buffer the soil pH to about 4·0. The leaf litterfall from the HF has a relatively low concentration of aluminium compared with that from the DF (M. Gautam-Basak & J. Proctor, unpublished) which occurs on less acid soils where the non-base saturation is probably mainly by Al^{+++} ions (I. C. Baillie, personal communication).

Although the scleromorphic leaves seem more likely to be an adaptation to low nitrogen than water stress it must be pointed out that heath forest has smoother canopies and smaller tree crowns than other forests (Whitmore 1975). Both these factors would tend to reduce water loss. It is possible that a reduction of transpiration is beneficial for plants in heath forest soils since it would reduce the mass-flow delivery to the root surface of potentially toxic hydrogen ions and possibly phenolic compounds. The latter have been shown to profoundly inhibit ion uptake by barley roots (Glass 1973, 1974) and are known to be relatively concentrated in heath forest leaf litterfall (Proctor *et al.* 1983).

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