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Phil. Trans. R. Soc. Lond. B 1992 **335**, 341-356
doi: 10.1098/rstb.1992.0026

Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition

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SUMMARY

Trees greater than or equal to 10 cm gbh were enumerated, mapped and identified in two 4 hectare (ha) (40 000 m^2) plots in 1985–1987. The number of species recorded was 511 (in 164 genera and 59 families) in a total sample of 17 985 individuals. Plots 1 and 2 contain 388 and 387 species respectively, and for trees greater than or equal to 30 cm gbh there are 247 and 242 species. Relative abundance patterns were fitted to a logseries distribution. In each plot, 51% of species are rare ($f < 5$) and 31% have only one tree ($f = 1$). Common species ($f \geqslant 5$) achieve a minimum area at 2 ha. The plots are close 'replicates' in many respects, and 8 ha gives an adequate sample.

The mean density of trees greater than or equal to 10 cm gbh and 30 cm gbh is 2248 ha^{-1} and 470 ha^{-1}, with corresponding basal areas of 30.7 $m^2\,ha^{-1}$ and 26.6 $m^2\,ha^{-1}$. The linear relation between ln frequency and ln gbh, the small (0.5%) ground area of gaps, and the low contribution by pioneer species show little recent disturbance. Dominance by 2–4 understorey species is pronounced.

For trees greater than or equal to 30 cm gbh, the Euphorbiaceae contribute the most to density at 21%, with Dipterocarpaeceae second at 16%: corresponding basal areas are 7% and 49%. For trees greater than or equal to 10 cm gbh, density of the Euphorbiaceae reaches 28%, Dipterocarpaceae 9%, followed by Annonaceae 8%, Lauraceae 7% and Meliaceae 6%. Lauraceae was the most species-rich family (83 species), then Euphorbiaceae (51 species) and Meliaceae (36 species).

Compared with the means of nine other sites in this forest type, Danum has 84% of the density and 74% of the basal area for trees greater than or equal to 30 cm gbh; and 60% of the species richness for this size class on a 1–1.6 ha basis. The forest is differentiated by its dominance by Euphorbiaceae, in terms of tree density, and the high contributions made by Lauraceae and Meliaceae. These attributes may reflect special site conditions and/or a late stage in recovery from past disturbance.

1. INTRODUCTION

In South-east Asia, lowland dipterocarp forest has been defined by Whitmore (1984) as a type of forest, within the lowland rain forest formation (i.e. dry lands up to 1200 m altitude), which is dominated in its upper and emergent canopy by the family Dipterocarpaceae. It is the most extensive forest type in Borneo.

To understand the processes which underlie spatial and temporal variations in patterns of species distribution within tropical rain forest requires intensive and detailed long-term observation. The means is by enumeration of a sufficiently large area of forest in which all trees of a chosen size class are accurately identified and are permanently labelled to enable their remeasurement with time. Two such demographic studies have been undertaken in lowland forest. At Sepilok, near Sandakan in Sabah (northern Borneo), Nicholson (1965) followed mortality and tree growth (1956–1962) in 2 hectares (ha)† of primary lowland dipterocarp forest (R.P. 17 Kabili-Sepilok Reserve (Fox 1973)), and at Sungai Menyala, in Peninsular Malaysia, Wyatt-Smith (1966) recorded mortality and recruitment (1947–1959) in a 2.02 ha plot of the same forest type, of which 1.62 ha was primary. This latter study was evaluated by Whitmore (1984), and recording was extended to 1981 by Manokaran & Kochummen (1987). In both enumerations the minimum gbh (girth at breast height) was 12 in (30.5 cm). Contemporaneous with the study reported here, a 50 ha plot, also in lowland dipterocarp forest, was set up at Pasoh in Peninsular Malaysia (Kochummen *et al.* 1990; Manokaran &

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† 1 ha = 10^4 m^2.

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Printed in Great Britain

LaFrankie 1990). All trees of greater than or equal to 1 cm dbh (diameter) or 3.1 cm gbh were enumerated.

Numerous other plots of differing areas and minimum gbh, and of varying degrees of completeness and accuracy in taxonomic identification of the trees, have been enumerated in tropical lowland forests of the region. But very few are exact enough for the purposes of ecological description at a site and quantitative comparison between sites, and for few of these were the trees labelled. Forest inventories often use many small plots and invariably group species, especially the non-commercial ones, approximately to family or genus level only, so that the data are of limited ecological use. Notably the Dipterocarpaceae have received the most detailed and accurate attention in all enumerations. Many other families of considerable ecological but little commercial interest (e.g. Euphorbiaceae) are poorly known.

Forest inventories and most ecological studies have usually recorded only trees of 10 cm dbh or more ($\geqslant$31.4 cm gbh) because this size class normally includes all canopy (overstorey) and emergent trees of species useful to forestry. No study except that at Pasoh (Kochummen *et al.* 1990; Manokaran & LaFrankie 1990) and the present one has attempted in an intensive way to enumerate and identify completely the smaller trees (less than 10 cm dbh) in a large (greater than 5 ha) area of lowland dipterocarp forest. A major deterrent has been the poorer taxonomic knowledge of these mostly understorey species. It has been commonly supposed that they have a relatively minor role in forest structure and functioning.

A new enumeration, besides including smaller trees and being as completely identified as possible, must be of sufficient contiguous area with regard to the following three considerations. Firstly, plots that are too small, possibly 1 ha in area or less, have insufficient numbers of trees of the abundant species from which statistically useful estimates of relative population sizes and rates of mortality and growth can be derived. Secondly, small plots are subject stochastically to large proportions of their area being naturally disturbed by tree falls. Thirdly, a plot which is large enough to enclose typical, local variation in topography and soils provides for greater generality of results and allows interesting comparisons within the plot.

Newbery & Proctor (1984), after classification of subplots within four 1 ha plots at Mulu, Sarawak, concluded that to detect variation in floristic composition relatable to edaphic change, replicated 2 ha to 4 ha plots were needed. Within-plot variation analysed by ordination of Nicholson's (1965) data at Sepilok, Sabah, by Austin & Greig-Smith (1968), suggested that 2 ha was sufficient to allow a topographical interpretation for the more common species. Poore (1968) detected patterns of scales of 50 m to 200 m in a 26 ha plot at Jengka, Peninsular Malaysia, enumerated for 19 abundant species of tree greater than or equal to 36 in (91.4 cm) gbh. These findings suggest that to contain variation in population density caused by dispersal, disturbance and edaphic differences, plots of 2 ha are minimal and 4 ha (or above) superior. Replication of plots is statistically more sound than one larger area because it provides the means to corroboration.

The three principal aims in setting up a large enumeration in the Danum Valley Conservation Area, Sabah, Malaysia (4°58′N, 117°48′E; see Marsh & Greer, this symposium) were: (i) to describe in detail forest structure and composition; (ii) to provide a permanent basis for long-term study of forest dynamics; and (iii) to investigate spatial patterning of the vegetation with respect to small-scale local topographic and edaphic variation. This would provide (i) a comparison with other studies (e.g. Pasoh); (ii) a 'base line' from which to judge the effects of recent disturbance by, and recovery from, logging in the neighbouring forests to the Conservation Area; and (iii) estimates of parameters for future modelling.

In this paper, analysis will be limited to the overall description of the forest in terms of basal area and density abundances, species richness, patterns of relative abundance and family composition; all of these can be compared with other lowland dipterocarp sites in the region.

2. THE SITE AND METHODS

(*a*) *Enumeration*

In a forest block *ca.* 40 ha in extent, and lying *ca.* 750 m west of the bridge over the Segama River near to the Danum Valley Field Centre, two 4 ha plots were qualitatively selected as being similarly representative of local topography and forest structure. No preliminary vegetation or floristic information was available to guide this choice.

Plots 1 and 2 (W of 1) lie parallel at *ca.* 280 m separation, their S.W. corners at 58 and 70 m elevation above the bed of the Segama respectively, or *ca.* 208 and 220 m ASL. Plots 1 and 2 contain a similar change in elevation, *ca.* 35 m, and have similar means and ranges in slope (*ca.* 23°, 10–35°) across 0.25 ha subplots. Plot 2 is traversed by a small seasonal stream. The soils of the area are a mixture of orthic acrisols and dystric cambisols (Bang association) lying on mudstone, sandstone and miscellaneous rocks (Wright 1975).

Field work began in July 1985. Plot 1 was enumerated between mid-September 1985 and mid-March 1986 (median date mid-December 1985), and plot 2 between mid-November and mid-December 1986 (median date mid-November 1986).

Each plot of dimensions 400 m (N) and 100 m (E) was gridded at 20 m intervals, with the corners of the 100 subplots permanently marked by belian posts. Disturbance to the plots was kept to the minimum. All living trees of 10 cm gbh or more were enumerated. Each tree was permanently tagged with an individually numbered (for the plot) aluminium disc, its position mapped to the nearest 0.1 m and the girth (gbh) measured over a paint mark on the bark at 1.3 m (bh) (girth was taken above any buttresses). Standing dead trees and fallen trunks (gbh $\geqslant$ *ca.* 75 cm) were recorded, and canopy gaps at ground level were mapped in 1986.

(*b*) *Tree identification*

Tree identification was undertaken in two phases.

1. 1985–1987. From each tree that could be climbed or reached freehand a botanical specimen was taken (two or more if it was fertile). For very common and reliably distinguishable taxa in the field (e.g. *Mallotus wrayi* King ex Hook. f.) this was not always necessary. Sorted representative subsamples of the taxa ($n = 20$ specimens for each, but where there were less than 20 all were kept) were named at Sabah Forest Department Herbarium at Sandakan with further confirmation of vouchers at the Royal Botanic Garden, Kew. Most of the botanical specimens were infertile, and it was impractical to store and retain all collected material. Large canopy and emergent trees were only identified in the field based on bark and fallen leaves.

2. 1988–1990. For the Dipterocarpaceae, all small trees were independently re-identified in the field in 1988 and the large trees were checked. In 1989, the surviving enumerated trees of all taxa were rechecked in the field (against phase 1 lists) together with further botanical collecting from unknown or uncertain taxa and for discrepant records. Trees that died were recorded: the annual mortality between the phases was 1.10% and 1.05%, over 40 and 28 months, for plots 1 and 2, respectively. Finally, a subsample of all but the rarest taxa in each plot were re-identified, inspected for consistency, and a further set of vouchers taken. Special attention was given to difficult families such as the Lauraceae.

All herbarium collections were collected and cross-referenced with field identifications at the Rijksherbarium, Leiden, to produce the final list and common set of voucher material. The internal consistency of the 20 specimens or fewer per taxon from phase 1 was re-assessed and found to be high. Corrected data files were complete by March 1991.

The underlying approach to the analysis of the data was to consider density and basal area in three size classes, namely 10 cm or more, 30 cm or more and 100 cm or more gbh.

3. SPECIES RICHNESS AND RELATIVE ABUNDANCE

(*a*) *Species richness*

Of a total of 511 taxa identified in the two plots

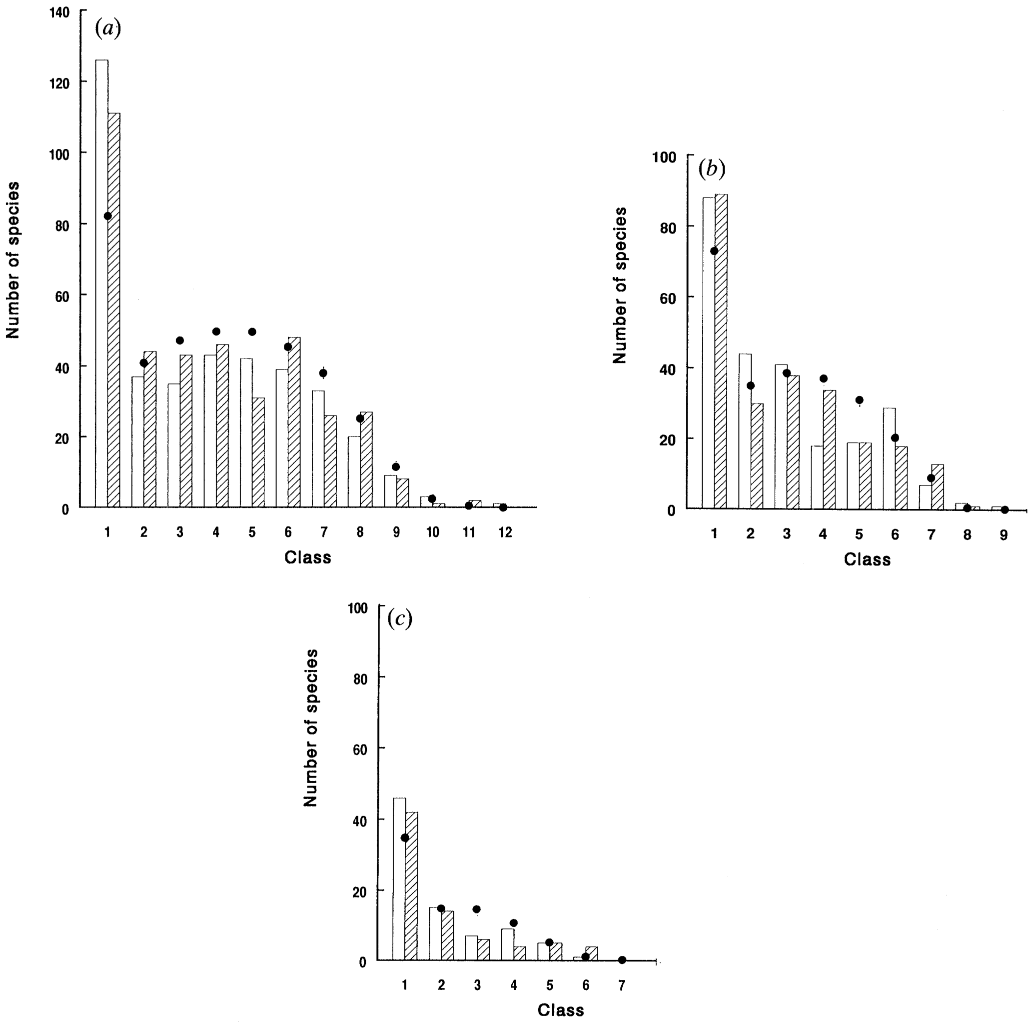

Figure 1. Frequency distributions of species in $\log_2$ abundance classes (number of trees per 4 ha plot) for three size classes of tree: (*a*) $\geqslant 10$ cm, (*b*) $\geqslant 30$ cm and (*c*) $\geqslant 100$ cm gbh. (Abundance intervals 1 1, 2 2, 3 3–4, 4 5–8, etc.) Plot 1 (open bars) and plot 2 (shaded bars); expected frequencies (mean of plots) for logseries distribution (circles).

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combined (table 1), 365 (71%) are to the species level and 146 (29%) are to the level of genus or above (118 (23%) to genus, 14 (3%) to family only and 14 (3%) to unknown family). All are recognized as distinct species. There are 59 families consisting of 164 genera. Identification depended largely upon infertile material with only 88 taxa (17%) having fertile vouchers, some of this flowering material coming from outside the plots. Apart from revision of names, phase 2 of the taxonomic work led to the correction in identification of 8.5% and 8.0% of the trees in plots 1 and 2, respectively. For the completed data set, 95% of taxa are to species or genus level in name and these represent 99.8% of the trees 10 cm gbh or more and practically 100% of the basal area.

Plots 1 and 2 consist of 388 and 387 species respectively for trees 10 cm gbh or more, 247 and 242 for trees 30 cm gbh or more, and 83 and 75 for trees 100 cm gbh or more. The Lauraceae is the most species-rich family (trees 10 cm gbh or more) with 83 species in 11 genera, followed by the Euphorbiaceae with 51 (17), Meliaceae 36 (7), Dipterocarpaceae 30 (6), Annonaceae 26 (11), Myrtaceae 26 (3), Burseraceae 20 (3), Rubiaceae 16 (13), Fagaceae 16 (3), Sapotaceae 11 (5), Anacardiaceae 14 (5), Leguminosae 14 (9), Myristicaceae 10 (3), and Xanthophyllaceae 10 (3). All other families have fewer than 10 species.

Species frequencies in the two plots are similarly distributed with respect to logarithmic ($\log_2$) abundance classes (number of trees in octaves) for trees 10 cm or more and 100 cm or more gbh ($\chi^2 = 14.4$, d.f. $= 8$, $p > 0.05$, < 0.1; $\chi^2 = 5.51$, d.f. $= 4$, $p > 0.05$, respectively) but the plots differed in their distributions for trees 30 cm gbh or more ($\chi^2 = 24.7$, d.f. $= 8$, $p < 0.001$). They show an increasingly concave shape with increasing minimum gbh, and a mode occurs at octave 4 (5–8 trees per species) for trees 10 cm gbh or more (figure 1). Because the differences between plots were small, only the means are given in table 1. Taxa with only one tree in a plot ($f = 1$) increase from *ca.* 30% to 50–60% of the total with increasing minimum gbh (10–100 cm) (table 1). Rare species (defined here as $f < 5$) increase over the same gbh range from *ca.* 50% to 80% (common species, $f \geqslant 5$, correspondingly decrease from 50% to 20%). The trends for the combined plot data are very similar (table 1). The logarithm of total number of species (plot means or combined) decreases approximately linearly with minimum gbh. Basal area per species, of trees 10 cm gbh or more, was lognormally distributed in plots 1 and 2 (cumulative probability scores correlations, $r = 0.993$ and 0.994 respectively, $p \ll 0.001$). For the two higher size classes there is evident truncation of a lognormal distribution corresponding to the minimum gbh used.

Table 1. *Numbers of rare (frequencies, $f = 1$ or $f < 5$) and correspondingly common ($f \geqslant 2$, $f \geqslant 5$) taxa in two 4 ha plots, and in the combined 8 ha, measures of diversity and evenness, and the degree of identification to 'genus/family only' on a percentage of taxa basis and contribution to total density and basal area, for trees ⩾ 10 cm, ⩾ 30 cm and ⩾ 100 cm gbh separately*

	⩾ 10 cm gbh		⩾ 30 cm gbh		⩾ 100 cm gbh	
	mean[a] (%)	combined (%)	mean[a] (%)	combined (%)	mean[a] (%)	combined (%)
number of taxa						
$f = 1$	119 (31)[f]	158 (31)	89 (36)	116 (24)	44 (56)	60 (50)
$f \geqslant 2$	269	353	157	220	35	61
$f < 5$	198 (51)	264 (52)	165 (67)	206 (61)	66 (82)	98 (80)
$f \geqslant 5$	190	247	81	130	14	24
all ($f \geqslant 1$)	388	511	246	336	79	121
diversity-A[b]	4.59	4.67	4.64	4.78	3.75	4.00
evenness-A[c]	0.75	0.72	0.84	0.82	0.86	0.83
diversity-B[d]	0.37	0.38	0.60	0.64	0.25	0.30
evenness-B[e]	8.01	8.10	12.93	13.57	6.05	7.48
percentage of taxa to 'genus/family only' with						
$f = 1$	43	47	31	34	33	33
$f \geqslant 2$	17	20	15	18	7	13
$f < 5$	37	43	27	30	25	28
$f \geqslant 5$	12	13	9	12	8	4
abundance of trees in taxa to 'genus family only'						
density/ha^{-1}	148 (6.6)		30 (7.2)		7 (11.1)	
basal area/(m^2 ha^{-1})	2.26 (7.4)		2.00 (7.5)		1.29 (7.2)	

[a] Differences in frequency between plots as percentage of mean: ⩾ 10 cm 0–5%, ⩾ 30 cm 0–6%, but for $f = 1$, 13%, ⩾ 100 cm 11–14%.

[b] Shannon index, H'.

[c] $H'/(\ln\ (\text{species richness}))$.

[d] Simpson index, $(1/D) \cdot 10^{-2}$.

[e] $(1/D)/H'$.

[f] Numbers in parentheses are percentages.

The expected frequencies of species with 1, 2, 3 . . . *n* individuals from the logarithmic series distribution are given by the terms

$\alpha x, \alpha x^2/2, \alpha x^3/3 \ldots \alpha x^n/n$

(May 1975; Pielou 1977; Magurran 1988), where x is the series constant and α the index of diversity. For trees 10 cm gbh or more, departure of the observed frequencies from those expected is highly significant ($\chi^2 = 32.4$ and 22.6, d.f. = 7, $p < 0.001$ and $p < 0.01$ for plots 1 and 2, respectively: $\alpha = 82.45$ both), but for trees 30 cm gbh or more ($\chi^2 = 23.9$ and 11.4, d.f. = 4, $p < 0.001$ and $p < 0.05$: $\alpha = 76.30$ and 74.88) and 100 cm gbh or more ($\chi^2 = 6.2$ and 12.4, d.f. = 2, $p < 0.05$ and $p < 0.01$: $\alpha = 44.47$ and 35.42) significance is slightly lower. For all size classes the general pattern is an over-representation of species with only one tree, especially pronounced for trees 10 cm gbh or more in plot 1 (contributing 74% of the χ^2), and an under-representation of intermediate classes (figure 1).

Excluding rare species, 'common species richness' (i.e. richness of species with $f \geqslant 5$, or with a density of one or more per ha) is 190 and 189 for plots 1 and 2, respectively, and the ratio of this new measure to (all) species richness is 0.49 for both plots.

(*b*) *Diversity and evenness*

Diversity and evenness (Hill 1973; Pielou 1977) based upon the Shannon index increases very slightly with increasing size class from 10 cm or more to 30 cm gbh or more (table 1); for 100 cm gbh or more, evenness remains similar but diversity decreases markedly. Plots differ little in these measures, by 2% of the mean at 10 cm or more and 30 cm or more and 6% for 100 cm or more classes. The Simpson index,

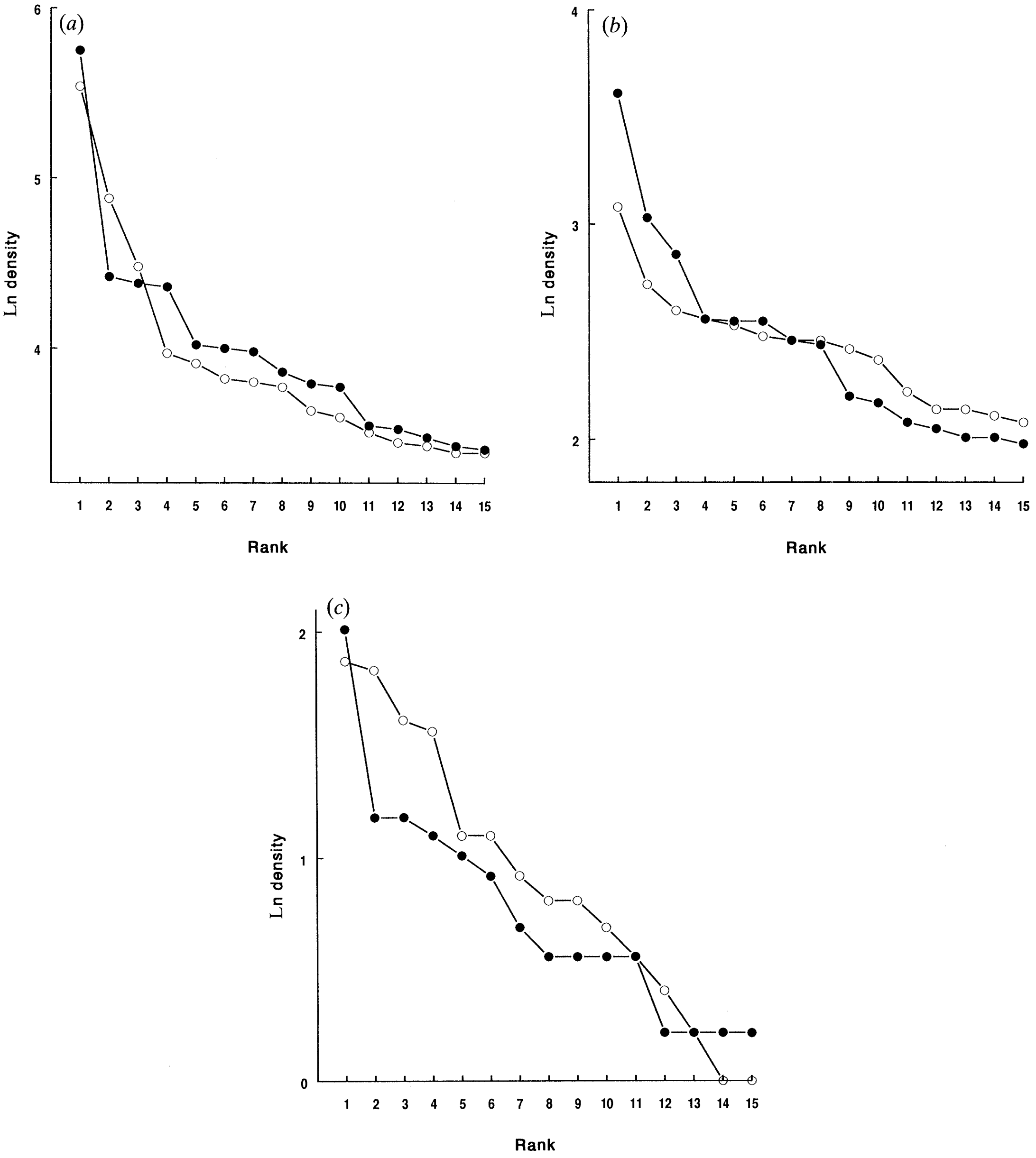

Figure 2. Ranked abundance (ln density) curves for three size classes of tree: (*a*) ⩾10 cm, (*b*) ⩾30 cm and (*c*) ⩾100 cm gbh, for the first 15 species in two 4 ha plots. Plot 1 (filled circles) and plot 2 (open circles).

which gives greater weight to more abundant species than does that of Shannon, emphasizes the lower diversity of the 10 cm or more and 100 cm or more classes (table 1), and a second measure of evenness based upon it shows the effect of decreased dominance in the 30 cm gbh or more class. Plots differ more noticeably with the Simpson index: 0.40 (units as table 1) in plot 2 and 0.33 in plot 1 for the 10 cm gbh or more size class, 0.66 and 0.54 for plots 2 and 1 respectively for the 30 cm gbh or more class, and 0.23 and 0.28 correspondingly for the 100 cm gbh or more class.

The logarithm of density plotted for the three size classes against the rank order of the 15 highest abundances shows a form (Whittaker 1970; May 1975) expected from the logseries model, with similar overall patterns for both plots (figure 2). The initial curvature becomes less pronounced with increasing minimum gbh. The differences in diversity and evenness between the size classes and plots is reflected in the differences in slope, especially for the first ten species. For trees 10 cm gbh or more there is strong dominance by 3–4 species, *Mallotus wrayi* King ex Hook. f. and *Dimorphocalyx muricatus* (Hook f.) Airy Shaw (Euphorbiaceae) among them in both plots, this being less so for trees 30 cm gbh or more, but one (*Shorea johorensis* Foxw.) and four species respectively for plots 1 and 2 assert dominance in the 100 cm gbh or more class (figure 2).

(*c*) *Level of identification*

Percentage taxa identified to species or to 'genus/family only' is similar for mean plot frequencies and the combined data. It declines slightly with increasing minimum gbh. For taxa represented by only one tree *ca.* 55% are identified to species, whereas for those with two or more trees *ca.* 80% are to species. Rare species were identified to species for *ca.* 60% of taxa and common species for 90% of taxa (table 1). Those taxa identified to 'genus/family only' represented 6–8% of the density or basal area of all taxa of trees 10 cm or more and 30 cm gbh or more. For trees 100 cm gbh or more they represent 11% of stems and 7% of the basal area.

(*d*) *Species–area relation*

The number of species occurring in each 20 m × 20 m subplot ($n = 100$ subplots per plot) was found for the three minimum gbh classes (10 cm or more, 30 cm or more and 100 cm or more) and three levels of exclusion of rarer species (none, $f = 1$ and $f < 5$ per plot). The mean number of species over both plots is 45 (range 21–71), decreasing to 44 and 42 on exclusion of species with only tree and rare species, respectively. Subplots of trees 30 cm gbh or more have the corresponding number of species as 15 (4–25), 14 and 12 and subplots of trees 100 cm gbh or more as 2.3 (0–7), 1.9 and 1.4. Plot 2 has slightly fewer taxa per subplot for trees 10 cm or more (by 2%) and 30 cm or more (by 7%) but slightly more for trees 100 cm or more (by 4%). There is no tree 100 cm gbh or more in 11 and 7 subplots of plots 1 and 2, respectively.

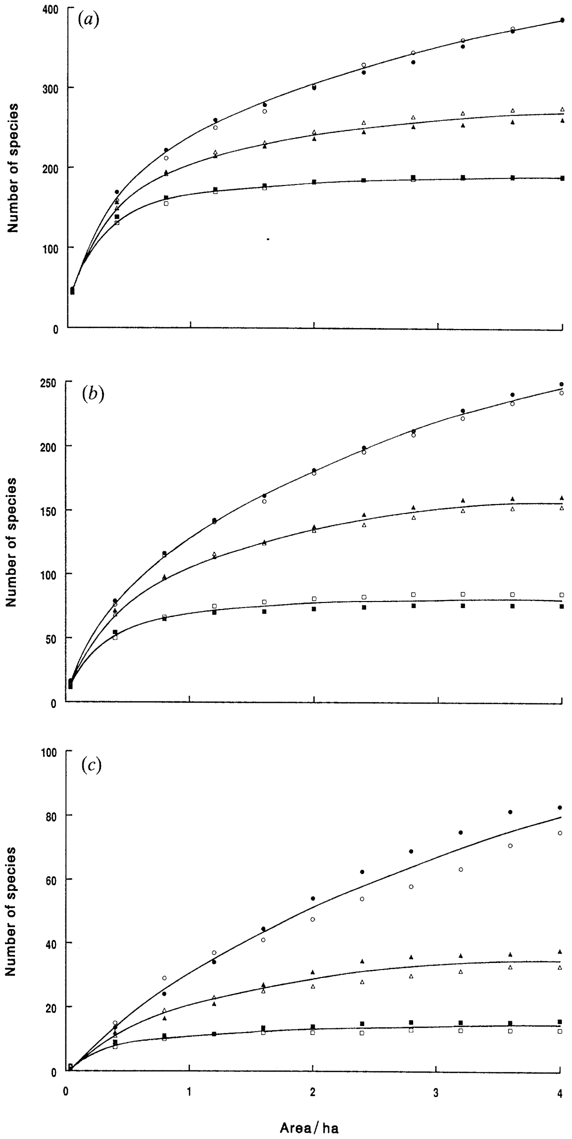

Figure 3. Cumulative increase in number of species with plot area for three size classes of tree: (*a*) ⩾ 10 cm, (*b*) ⩾ 30 cm and (*c*) ⩾ 100 cm gbh, and three levels of exclusion of less common species. Curves fitted by hand through the means for plots 1 and 2. All species (filled circles, open circles); $f \geqslant 2$ (filled triangles, open triangles); $f \geqslant 5$ (filled squares, open squares) (plots 1 and 2, respectively).

For all three size classes, the cumulative number of species continues to increase as plot area increases to 4 ha showing no decrease in slope to zero (figure 3). (These data are derived from the means of two runs, moving row by row, one from S.W. to N.E. corners of each plot and the other vice versa.) Between 2 ha to 4 ha the slope is approximately linear and the rate of accumulation 43, 33 and 15 species per hectare for the three increasing size classes respectively. Excluding species with only one tree in a plot ($f = 1$) the rate of accumulation is less steep but begins to reach a slope of zero at *ca.* 4 ha. When rare species ($f < 5$) are excluded, however, the rate decreases to near zero at *ca.* 2 ha (figure 3). By 1 ha, 88% of common species ($f \geqslant 5$) of trees 10 cm gbh or more have accumulated, and correspondingly 87% of common species 30 cm gbh or more and 76% of such species 100 cm gbh or more. The minimal area for common species is therefore close to 2 ha.

4. DENSITY AND BASAL AREA ABUNDANCE

(*a*) *Comparison of plots*

Of the 9002 trees enumerated in plot 1, 24 died between tagging and identification and three were missing (a 0.3% loss), and of the 8983 trees enumerated in plot 2, 15 died and none was missing (a 0.2% loss). Nearly 80% of the enumerated trees are less than 30 cm gbh, but only 3% exceed 100 cm gbh (table 2). The two plots show very similar densities of trees less than 30 cm gbh. For trees 30 cm gbh or more, plot 2 has 8% fewer trees 30–100 cm gbh, but 10% more trees 100 cm gbh or more than plot 1. The number of trees standing or lying dead is 11 per ha, i.e. *ca.* 10% of the size-class alive. Of the total basal area, trees 30 cm gbh or more account for 87%, and of this 58% is for trees 100 cm gbh or more (table 2). In plots 1 and 2, 20 and 19 trees, respectively, are 300 cm gbh or more, and 6 and 1 are 400 cm gbh or more. The largest tree was a dipterocarp (*Shorea pauciflora* King) 554 cm gbh (2.44 m^2 basal area) in plot 1.

Table 2. *Density and basal area of trees in three size classes in plots 1 and 2, and the representation of the most abundant taxa, with the contribution by pioneers, the numbers of dead trees, and gaps*

	plot			
	1	2	mean	%
density of trees/ha^{-1}				
$\geqslant 10$ cm gbh	2250	2246	2248	
$\geqslant 10$, < 30 gbh	1766	1791	1778	79
$\geqslant 30$ gbh	484	455	470	21
$\geqslant 30$, < 100 gbh	423	389	407	18
$\geqslant 100$ gbh	61.0	65.5	63.3	3
basal area/(m^2 ha^{-1})				
$\geqslant 10$ cm gbh	30.48	30.97	30.73	
$\geqslant 10$, < 30 gbh	4.12	4.18	4.15	13
$\geqslant 30$ gbh	26.36	26.79	26.58	87
$\geqslant 30$, < 100 gbh	9.07	8.22	8.65	28
$\geqslant 100$ gbh	17.29	18.57	17.93	58
density of trees $\geqslant 10$ cm gbh represented by:				
1° 30 taxa	1329	1294	1312	58
1° 50 taxa	1602	1598	1600	71
basal area of trees $\geqslant 10$ cm gbh represented by:				
1° 30 taxa	21.38	21.17	21.28	69
1° 50 taxa	24.20	24.52	24.36	79
pioneers[a]				
density/ha^{-1}				
$\geqslant 10$ cm gbh	76	65	70	3.1
$\geqslant 30$ cm gbh	23	13	18	3.8
basal area/(m^2 ha^{-1})				
$\geqslant 10$ cm gbh	0.84	0.44	0.64	2.1
number of dead trees/ha^{-1} ($\geqslant$ *ca.* 75 cm gbh)	11	12	11	
gaps				
number per plot	3	9	6	
total gap area/m^2	208	184	196	
% plot area	0.52	0.46	0.49	

[a] Percentage of totals per plot.

(*b*) *Size frequency distributions*

The relation between logarithmic (ln) frequency of trees and ln gbh is also very similar for plots 1 and 2, the slopes of the fitted lines differing by less than 0.05 (i.e. $< 2\%$) for both ranges of gbh used (figure 4*a*). The average plot frequencies decline more steeply, with increasing gbh. Considering trees in the range 90–170 cm gbh, the deviations in ln frequency from the common line for plots 1 and 2 are significantly correlated ($r = 0.94$, d.f. $= 6$, $p < 0.001$).

Logarithmic frequency of trees in the Dipterocarpaceae (averaged for the plots) declines linearly with increasing lngbh (range 10–60 cm) but it declines as a quadratic function of lngbh for the Euphorbiaceae (figure 4*b*). The slopes differ by 0.03 (1%) when dipterocarps were considered separately for each plot: the plots are very similar in the curved response for the euphorbs (figure 4*b*).

(*c*) *Gaps and pioneers*

The mean percentage area of plots as open (ground) gaps is 0.5% (table 2). Plots 1 and 2 have similar total gap areas but the gaps are smaller and more frequent in plot 2 than plot 1. Combining the data for both plots, the mean individual gap area was 23 m^2 (95% confidence limits: 13 m^2 and 40 m^2, $n = 12$; ln transformed data).

In the plots, 28 species are putative pioneers (T. C. Whitmore, personal communication) forming *ca:* 3% of the trees 10 cm gbh or more (table 2). Plot 1 has almost twice the density of pioneer trees 30 cm gbh or more (eight and two trees in plots 1 and 2, respectively, were 100 cm gbh or more) and twice the basal area (10 cm gbh or more) of plot 2.

(*d*) *Constancy*

Considering both plots together ($n = 32$ subplots of 0.25 ha), 33% of all species of trees 10 cm gbh or more occur in only one subplot, whereas 80% occur in 16 subplots or fewer (figure 5). Of the 20% in 17 subplots or more, half of these occur in 25 subplots or more, with 15 species (3%) in all 32 subplots. For trees 30 cm gbh or more, 37% of taxa occur in only one subplot, 90% in 16 or fewer. Of that 10% in 17 subplots or more, 12 were in 25 subplots or more and only one, the euphorb (*Mallotus wrayi*), in all 32.

Table 3. *Basal area ($m^2\ ha^{-1}$) of trees $\geqslant$10 cm gbh of the first 15 families, ranked in terms of basal area in plots 1 and 2 separately then combined, with the mean and overall percentage contributions (where $\geqslant$2%); and the mean plot basal area of the same families for trees $\geqslant$30 cm and $\geqslant$100 cm gbh and their percentage contributions*

(Values for basal areas in parentheses indicate that the family was not in the 15 for that plot; o, u or i indicate a family is overstorey, understorey or intermediate between storeys; * a special case.)

		⩾10 cm gbh				⩾30 cm gbh		⩾100 cm gbh	
family	storey	plot 1	plot 2	mean	%	mean	%	mean	%
Dipterocarpaceae	o	12.74	14.10	13.42	43.7	13.10	49.1	11.87	65.8
Euphorbiaceae	u	3.37	2.87	3.12	10.2	1.84	6.9	0.17	—
Lauraceae	o	2.02	1.53	1.78	5.8	1.49	5.6	0.94	5.2
Myrtaceae	o	1.61	1.07	1.34	4.4	1.19	4.5	0.64	3.5
Olacaceae	o	0.74	1.72	1.23	4.0	1.19	4.5	0.97	5.4
Meliaceae	o	1.47	0.90	1.19	3.8	0.95	3.6	0.22	—
Fagaceae	o	1.07	0.92	1.00	3.3	0.94	3.5	0.50	2.8
Annonaceae	i	1.06	0.76	0.91	3.0	0.57	2.1	0.02	—
Leguminosae	*	0.53	1.14	0.84	2.7	0.68	2.6	0.61	3.4
Sapotaceae	o	1.06	0.57	0.82	2.7	0.70	2.6	0.30	—
Tiliaceae	o	0.80	0.55	0.68	2.2	0.61	2.3	0.13	—
Burseraceae	o	0.68	0.34	0.51	—	0.44	—	0.23	—
Lecythidaceae	o	0.35	0.51	0.43	—	0.41	—	0.06	—
Verbenaceae	o	(0.00)	0.54	0.27	—	0.26	—	0.20	—
Thymelaeaceae	o	0.24	(0.29)	0.27	—	0.23	—	0.13	—
Xanthophyllaceae	i	(0.13)	0.29	0.21	—	0.15	—	0.01	—
Melastomataceae	i	0.21	(0.13)	0.17	—	0.12	—	0.04	—
sum first 17 families		28.05	28.23	28.14	92	24.83	93	17.04	95
other families[a] ($n=42$)		2.43	2.74	2.59	8	1.75	7	0.89	5
total ($n=59$)		30.48	30.97	30.73		26.58		17.93	

[a] Including 14 taxa not known to family level.

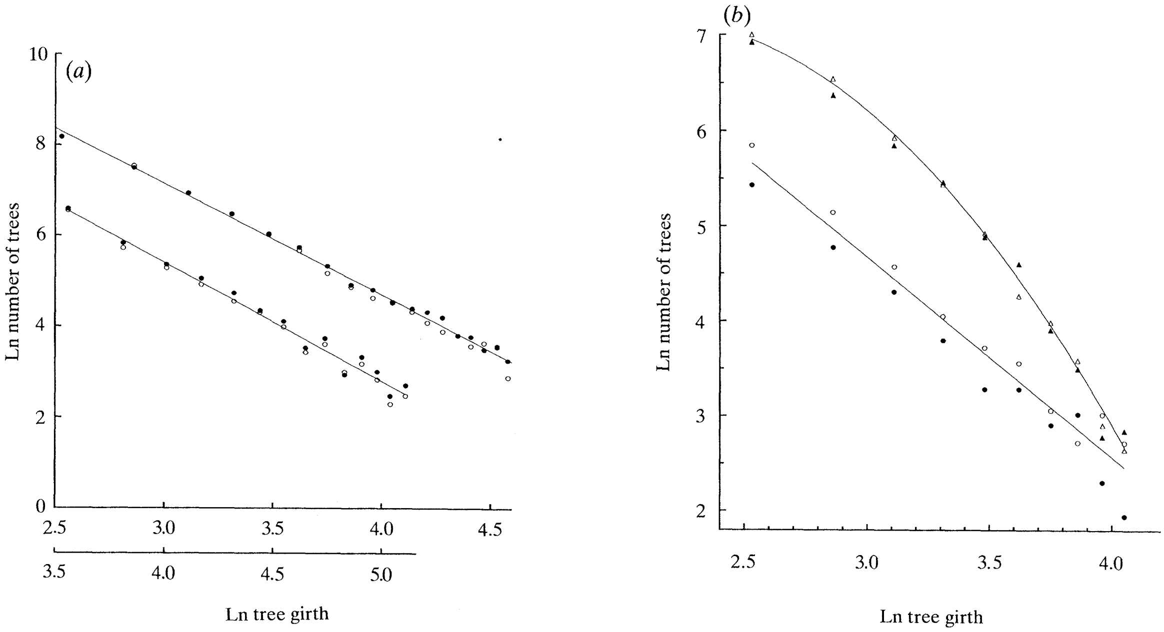

Figure 4. Frequency distributions of trees per plot in increasing gbh classes. (*a*) All trees, in two segments; 10–100 cm (upper line; $\ln(N) = 14{\cdot}5 - 2{\cdot}45 \ln(\text{gbh})$) with 5 cm interval ($r^2 = 0.99$, both plots); 30–170 cm (lower line; $\ln(N) = 15{\cdot}8 - 2{\cdot}60 \ln(\text{gbh})$) with 10 cm interval ($r^2 = 0.98$, both plots). Plot 1 (filled circles) and plot 2 (open circles). (*b*) Trees in Dipterocarpaceae (filled circles, open circles), and Euphorbiaceae (filled triangles, open triangles), range 10–60 cm gbh with 5 cm interval (r^2 range = 0.95–0.98). Upper line, $\ln(N) = 1{\cdot}93 + 4{\cdot}88 \ln(\text{gbh}) - 1{\cdot}16 (\ln(\text{gbh}))^2$; lower line, $\ln(N) = 10{\cdot}8 - 2{\cdot}06 \ln(\text{gbh})$.

5. FAMILY COMPOSITION

(*a*) *Similarity between plots*

The 15 most abundant families in terms of basal area of trees 10 cm gbh or more in plot 1 were combined with the 15 similar families in plot 2. The joint list, in table 3, contains 17 families with 13 out of 15 (87%) in common and has a significantly correlated rank ordering of abundances ($r_s = 0.80$, d.f. = 15, $p < 0.001$). A similar tabulation was made for trees

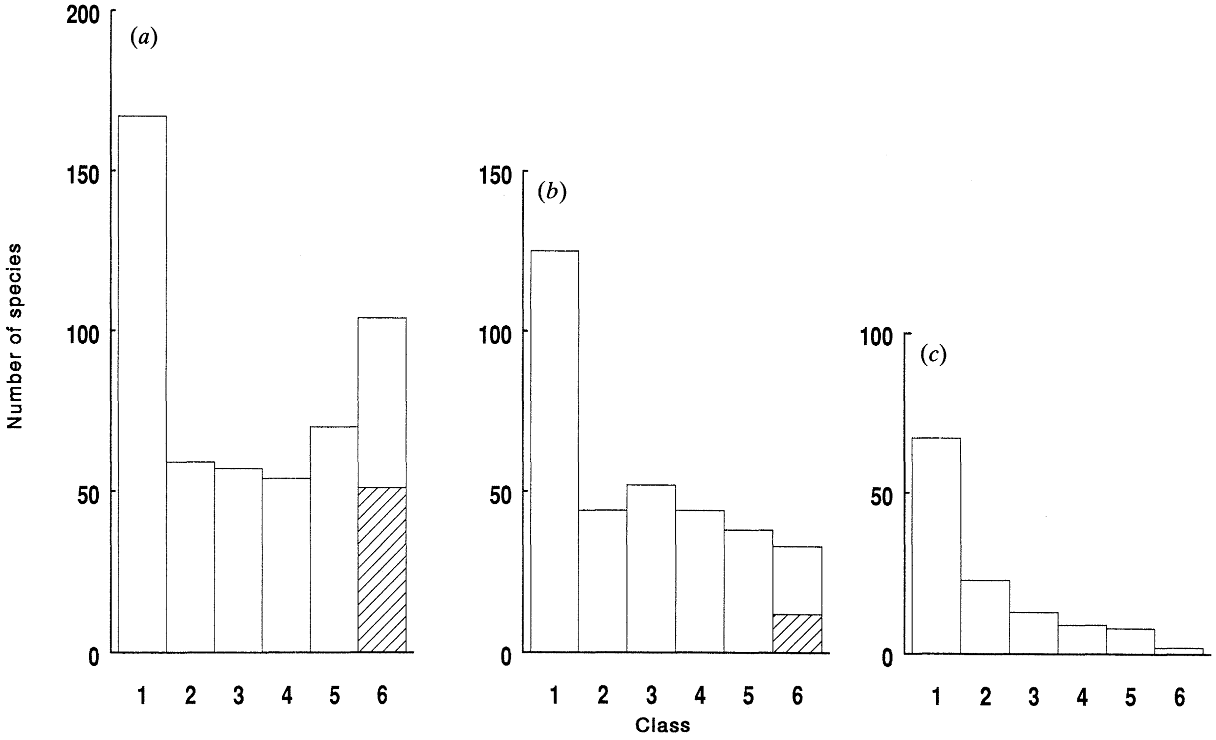

Figure 5. Subplot (0.25 ha) frequency distribution of species in $\log_2$ frequency of occurrence (out of 32) classes (class intervals as for figure 1; shaded area of last class 25–32) for three size classes of tree: (*a*) $\geqslant 10$ cm, (*b*) $\geqslant 30$ cm, and (*c*) $\geqslant 100$ cm gbh.

30 cm gbh or more, which resulted in 16 families all of which were in the 10 cm gbh or more list. The rank ordering between size classes (using the means of the two plots for each class) is more highly correlated ($r_s = 0.98$, d.f. = 15, $p < 0.001$) than that between plots.

Finding the ratios of basal areas of trees 30 cm gbh or more to the total (i.e. of trees 10 cm gbh or more), 13 out of 17 (76%) have greater than 80% of the total basal area contributed by trees 30 cm gbh or more. The ratios for the other four families were: Xantho-

Table 4. *Densities* (*ha*$^{-1}$) *of trees* $\geqslant 10$ *cm gbh of the first 15 families, ranked in terms of density in plots 1 and 2 separately, then combined, with the mean overall percentage contributions* (*where* $\geqslant 2\%$)*; and the mean plot density of the same families for trees* $\geqslant 30$ *cm and* $\geqslant 100$ *cm gbh and their percentage contributions.*

(Values in parentheses indicate that the family was not in the 15 for that plot; o, u and i indicate a family is overstorey, understorey or intermediate between storeys.)

		$\geqslant 10$ cm gbh				$\geqslant 30$ cm gbh		$\geqslant 100$ cm gbh	
family	storey	plot 1	plot 2	mean	%	mean	%	mean	%
Euphorbiaceae	u	603	635	619	27.5	97	20.6	1.3	2.1
Dipterocarpaceae	o	176	243	210	9.3	76	16.2	27.1	42.8
Annonaceae	i	205	139	172	7.7	29	6.1	0.3	—
Lauraceae	o	165	138	152	6.7	32	6.8	4.5	7.1
Meliaceae	o	153	131	142	6.3	35	7.5	1.8	2.8
Myrtaceae	o	108	76	92	4.1	27	5.7	3.8	6.0
Leguminosae	o	92	66	79	3.5	5	—	1.6	2.5
Rubiaceae	u	79	69	74	3.3	4	—	0.0	—
Myrsinaceae	u	55	92	74	3.3	6	—	0.0	—
Sapotaceae	o	87	53	70	3.1	17	3.6	2.4	3.8
Tiliaceae	o	55	42	49	2.2	21	4.4	1.1	—
Fagaceae	o	48	42	45	2.0	20	4.3	3.2	5.1
Burseraceae	o	38	45	42	—	12	2.5	1.5	2.4
Flacourtiaceae	u	31	47	39	—	5	—	0.0	—
Xanthophyllaceae	i	(28)	39	34	—	7	—	0.1	—
Olacaceae	o	32	(34)	33	—	10	2.8	5.3	8.4
sum of first 16 families		1955	1891	1923	86	402	86	54.0	85
other families[a] ($n = 43$)		295	355	325	14	68	14	9.3	15
total ($n = 59$)		2250	2246	2248		470		63.3	

[a] Including 14 taxa not known to family level.

phyllaceae 0.71; Melastomataceae 0.71; Annonaceae 0.63; and Euphorbiaceae 0.59. A comparison between plots of the basal area of trees 30 cm gbh or more shows that they differ in similar proportions to the 10 cm gbh or more basal areas. For trees 100 cm gbh or more (table 3) the pattern of distribution of basal area with families is different from the two smaller size classes (compared with 10 cm or more list, $r_s = 0.71$; and with 30 cm or more list, $r_s = 0.77$; both d.f. = 15, $p < 0.01$).

Selection of the first 15 most abundant families in terms of densities of trees 10 cm gbh or more in each plot separately resulted in 16 families in a joint list (14 out of 15, 93% in common; $r_s = 0.90$, d.f. = 14, $p < 0.001$; table 4). Tabulation of densities for trees 30 cm gbh or more shows less agreement for the first 15 ranked in each plot with only 12 in common (80%) in a joint list of 18 families. Of the 10 cm gbh or more list, all are present in the 30 cm gbh or more list showing a high degree of agreement in the presence of these two size classes, although the relative abundances were more variable ($r_s = 0.68$, d.f. = 14, $p < 0.05$). However, unlike basal area, the ratios of densities of trees 30 cm gbh or more to the total varies greatly between families from 0.05 to 0.6, with 6 out of 16 (38%) less than 0.20 and 10 out of 16 (62%) 0.20 or more. Tree densities are therefore usefully considered separately for the 10 cm gbh or more and 30 cm gbh or more data. The distribution of families in terms of density of trees 100 cm gbh or more is more distinct (compared with the 10 cm or more list, $r_s = 0.20$; with the 30 cm or more list, $r_s = 0.53$; both d.f. = 14, $p > 0.05$; table 4).

(*b*) ***Basal area contribution***

The Dipterocarpaceae is the most abundant family in both plots, contributing on average 44% of the total basal area for trees 10 cm gbh or more. Euphorbiaceae and Lauraceae are the next most abundant, bringing the total for these three families to 60% (table 3). The plots differ in family representation: plot 1 has greater abundances of Euphorbiaceae, Lauraceae, Myrtaceae, Meliaceae and Sapotaceae, whereas plot 2 is greater in Dipterocarpaceae, Olacaceae and Leguminosae. For trees 30 cm gbh or more, Dipterocarpaceae contribute 49% basal area, with the Euphorbiaceae and Lauraceae bringing the total to 62%. Annonaceae and Rubiaceae are lower ranked than for the 10 cm gbh or more data. Dipterocarpaceae contribute 66% of the basal area of trees 100 cm gbh or more, with Olacaceae and Lauraceae bringing the total to 77%. Euphorbiaceae, Rubiaceae and Annonaceae are noticably very low or absent from the 100 cm gbh or more list (table 3).

(*c*) ***Density contribution***

In terms of densities of trees 10 cm gbh or more, the Euphorbiaceae contributes markedly the most trees (28%) with the Dipterocarpaceae in second place (9%). Three other families with high densities of small trees are Annonaceae, Lauraceae and Meliaceae (table 4). With increasing minimum gbh to 30 cm the Euphorbiaceae decrease, and the Dipteroarpaceae increase their contribution (to 21% and 16%, respectively) and at 100 cm or more the latter form 43% of trees and the former negligible numbers. Annonaceae, Rubiaceae and Myrsinaceae all decrease in ranking with minimum gbh (table 4). Olacaceae markedly increases its contribution to total density as minimum gbh changes from 10 cm or more to 100 cm or more, Leguminosae decreases for 30 cm gbh or more but increases again for 100 cm gbh or more. Lauraceae and Myrtaceae remain relatively constant in rank position, whereas Burseraceae, Sapotaceae and Fagaceae fluctuate in an intermediate band of rankings. These changes reflect the relative size contributions of the different families.

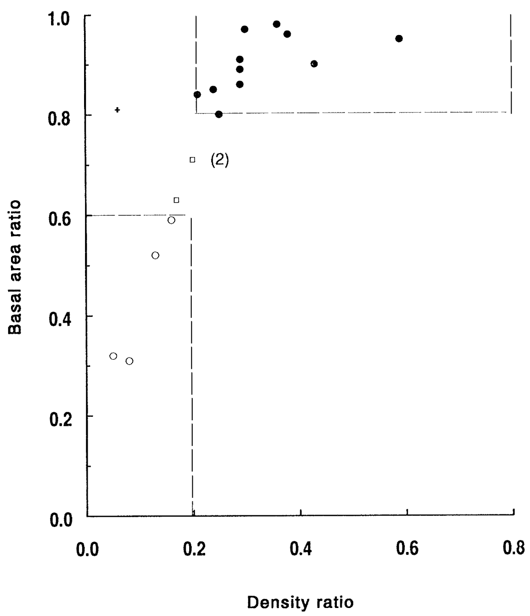

Figure 6 . Relation between the ratio of basal area for trees $\geqslant 30$ cm gbh to that for trees $\geqslant 10$ cm gbh, and the same for densities, indicating predominantly overstorey (filled circles), understorey (open circles) and intermediate-storied (open squares) families; +, a special case.

(*d*) ***Structural classification***

The family lists for trees 10 cm gbh or more for basal area and for density data (tables 3 and 4) were further combined to give 20 families in common. Further basal area and density ratios ($\geqslant 30$ cm/$\geqslant 10$ cm gbh) were calculated for the additional families. The relation between basal area and density ratios (figure 6) shows a classification into 12 overstorey families (basal area ratio > 0.80, density ratio > 0.20 (to 0.6)), four understorey families (basal area ratio < 0.60, density ratio < 0.20), and three intermediately placed families of which the Leguminosae is a special case with an under-overstorey bimodality.

6. COMPARISONS WITH OTHER SITES

(*a*) ***Density and basal area abundance***

Density and basal area of trees greater than or equal to 30.0/31.4 cm gbh (averaged from table 5; equivalent to 10 cm dbh or more and similar to 12 in

(30.5 cm) or more gbh) in the Danum plots (table 5) are 84% and 74%, respectively, lower than the means of nine other sites in Peninsular Malaysia and Borneo (mean ± s.e. density, 537 ± 43 and basal area, 35.8 ± 3.1; excluding other Danum plot). Assuming a random sample, the difference in densities is insignificant ($t = 1.98$, d.f. $= 8$, $p > 0.05$) but that for basal area is significant ($t = 3.02$, d.f. $= 8$, $p < 0.05$). Density of trees at Danum (using 30 cm or more values) is 23% less than that at Sepilok, and the basal area is 30% less. Compared with Segaliud-Lokan, Danum has a 66% higher density but a 6% lower basal area. For one other plot at the Danum, *ca.* 0.5 km west of the two described here, Kamarudin (1986) had an 8% lower density but 61% greater basal area of trees 10 cm dbh or more. The Danum plots were closest to Lempake in East Kalimantan in terms of density, and to Pasoh, Peninsular Malaysia, in terms of basal area (table 5). Density of trees 10 cm gbh or more at Danum was very close to that estimated for Pasoh (table 5).

Ashton (1964) stratified his sampling into 20 valley, 15 hillside and 15 ridge plots (each *ca.* 0.4 ha). The mean density and basal area of trees 12 in (30.5 cm) gbh or more were found here by summing *de novo* all species records given in Ashton's tables. The sample is not random: valley plots are over-represented (P. S. Ashton, personal communication) relative to their occurrence. Values for Andalau are close to those for Sepilok.

Burgess (1961) refers to earlier work by Nicholson who 'as a result of his study of 19 acres contained in five jungle plots distributed throughout the Colony' found a density of 480 per ha and a basal area of 39.0 m^2 per ha for trees 12 in (30.5 cm) gbh or more, this latter value being considerably higher than that for the Danum. The Sabah Forest Department (1987) also report on a 120 ha enumeration in progress at Sapulut, near Kengingau in Sabah, with an average density of trees 10 cm dbh or more (31.4 cm gbh or more) of *ca.* 670 per ha, again greater than the density at Danum (table 5).

Density and basal area of trees 91.4 cm (36 in) gbh or more was lower on average by 32% and 21%, respectively, at Danum than on the two Jengka plots in Peninsular Malaysia (table 5), although similar in density to, but lower in basal area than, Segaliud-Lokan for trees 152.4 cm (60 in) gbh or more. Compared with the plots at Andalau for trees 48 in (121.9 cm) gbh or more, the density and basal area at Danum are again lower by 27% and 15%, respectively.

Table 5. *Comparison of basal area and density of trees in two 4 ha plots at Danum with those at other sites for five size classes of tree*

	area/ha (over ground)	minimum gbh/cm	density/ha^{-1}	basal area/(m^2 ha^{-1})	reference
Sepilok (R.P.17), Sabah	2.0	30.5	608	37.8	Nicholson (1965)
Segaliud-Lokan, Sabah	2.83[a]	30.5	283	28.4	Fox (1967)
Silam, Sabah	0.8[b]	31.4	573	42.2	Proctor *et al.* (1988)
Danum Valley, Sabah	1.0	30.0	431	42.8	Kamarudin (1986)
Andalau, Brunei	20.2[c]	30.5	628	35.2	Ashton (1964: App. 3, table 13)
Mulu, Sarawak	1.0	31.4	739	57.0	Proctor *et al.* (1983)
Wanariset, E. Kalimantan	1.6	31.4	541	29.7	Kartawinata *et al.* (1981)
Lempake, E. Kalimantan	1.6	31.4	445	33.7	Riswan (1987)
Sungai-Menyala, Pen. Malaysia	1.62	30.5	488	32.9	Wyatt-Smith (1966)
Pasoh, Pen. Malaysia	50.0	31.4	530	25.2	Manokaran & LaFrankie (1990)
present study	8.0	(30.0)	470	26.6	
		(31.4)	434	26.3	
Jengka, Pen. Malaysia					
(a)	24.0	91.4	121	24.2	Poore (1968)
(b)	11.7	91.4	104	23.3	Ho *et al.* (1987)
present study	8.0	91.4	76	18.8	
Andalau, Brunei	20.2[c]	121.9	70	19.0	Ashton (1964: table 17*a*)
present study	8.0	121.9	44	16.1	
Segaluid-Lokan, Sabah	31.9[d]	152.4	31	16.9	Fox (1967)
present study	8.0	152.4	29	13.8	
Pasoh, Pen. Malaysia	50.0	10.0	2210[e]	—[f]	Manokaran & LaFrankie (1990)
present study	8.0	10.0	2248	30.7	

[a] 35 × 0.2 acre plots.
[b] 2 × 0.4 ha plots.
[c] 50 × *ca.* 0.4 ha plots.
[d] 394 × 0.2 acre plots.
[e] Estimated from a ln (N) against ln (gbh) graph.
[f] Not known.

Table 6. *Comparison of the number of species in two 4 ha Danum plots with other sites for the same plot area and size class of trees*

(Trees ⩾12 in (=30.5 cm) gbh, ⩾10 cm dbh (=31.4 cm gbh) and ⩾30.0 cm gbh taken as equivalent.)

		number of species		
site	area/ha	compared site	Danum Valley	reference
plots ⩾1, <4 ha, gbh ca. 30 cm[a]				
Sepilok, Sabah	2.0	198	180	Nicholson (1965)
Wanariset, E. Kalimantan	1.6	239	160	Kartawinata *et al.* (1981)
Lempake, E. Kalimantan	1.6	209		Riswan (1987)
Sungei-Menyala, W. Malaysia	1.6	210		Wyatt-Smith (1966)
Danum Valley, Sabah	1.0	124	128	Kamarudin (1986)
Mulu, Sarawak	1.0	214		Proctor *et al.* (1983)
Pasoh, W. Malaysia	1.0[b]	210		Kochummen *et al.* (1990)
plots ⩾4 ha, gbh ca. 90 cm				
Jengka, W. Malaysia			90	
(a)	4.0	160		Poore (1968; figure 4)
(b)	4.0	140		Ho *et al.* (1987; figure 2)

[a] Danum Valley equivalent read from figure 3*b*.

[b] Mean of 50 1 ha subplots.

(*b*) *Species richness and relative abundance*

The two Danum plots are mostly less species rich for trees 30 cm gbh or more than the six other sites with which they can be compared in table 6, being 90% of the value for Sepilok, 71% of the two East Kalimantan sites, 69% on average of Sungei Menyala and Pasoh, and 60% of the Mulu, Sarawak site. On average the Danum plots have 60% of the species number accumulated in 4 ha of the two Jengka plots for trees 91.4 cm (60 in) gbh or more (table 6). At Danum, on a 1 ha basis, Kamarudin (1986) recorded a very similar species richness to that in the two plots analysed here.

Limiting comparisons to the most statistically reliable values (namely three 1.6 ha plots taken together, and the average of 50 subplots of 1 ha at Pasoh) for trees 30 cm gbh or more, the Danum has 60% of the species richness of these other sites.

Nicholson (1965) found that 30% and 70% of the species of tree 30.5 cm (12 in) gbh or more at Sepilok had only one tree ($f=1$) and were rare ($f<5$), respectively. Comparable values for the dipterocarp forest at Mulu (trees 10 cm dbh or more, or 31.4 cm gbh or more) were 47% and 77%, respectively (J. Proctor, personal communication). These approximate to the Danum values of 36% and 67% of species having only one tree and rare species, respectively (trees 30 cm gbh or more; table 1). At Jengka, Poore (1968) showed 37% and 66% of species, and Ho *et al.* (1987) 47% and 76% of species, had only one tree and were rare, which compares with 54% and 79%, respectively, for the Danum plots when trees 91.4 cm (36 in) gbh or more are considered.

Species richness in families varies with the area enumerated and the minimum gbh. Nevertheless, the ten richest families for trees 30 cm gbh or more at Danum (mean of two 4 ha plots) can be compared approximately with the same families at Sepilok (Nicholson 1965; 2 ha plot, trees 30.5 cm gbh or more; 44 families) and at Lempake (Riswan 1987; 1.6 ha plot, trees 31.4 cm gbh or more; also 44 families) in that order: Lauraceae (34, 9, and 18 species), Euphorbiaceae (25, 24, 32), Dipterocarpaceae (19, 21, 12), Meliaceae (18, 7, 12), Myrtaceae (15, 16, 8), Annonaceae (13, 6, 22), Leguminosae (10, 8, 6), Fagaceae (9, 7, fewer than 3), Burseraceae (9, 8, 8) and Rubiaceae (8, 12, 15). At Wanariset (Kartawinata *et al.* 1981; area and minimum gbh as Lempake; 45 families) the first four families last listed have 14, 26, 14 and 13 species, respectively. Fox (1967) reported (several small plots combined, trees 30.5 cm gbh or more) '... a large number of species grouped in the families Euphorbiaceae, Lauraceae and Annonaceae...'. At Pasoh (Kochummen *et al.* 1990; 50 ha plot, trees 1 cm dbh or more or 3.1 cm gbh or more; 78 families) the species richness of the first five ranked families was Euphorbiaceae (87), Myrtaceae (50), Lauraceae (48), Rubiaceae (46) and Annonaceae (44). The distinctive feature of the Danum site, therefore, is the very high species richness of the Lauraceae and a relatively species-rich Meliaceae.

(*c*) *Family composition*

Limiting comparisons to North-east and East Borneo (table 7) avoids large biogeographical differences within Malesia. Based on the densities of trees 30 cm gbh or more (i.e. 12 in gbh and 10 cm dbh), six families making the largest contributions at each site were combined to give a joint list of 14 families. (No data exist in the literature to permit comparisons for trees 10 cm gbh or more.) Two families which have a greater than 2% contribution in only one non-Danum site are excluded (table 7). Danum, in common with Lempake, has almost twice the contribution by Euphorbiaceae than the other sites. Dipterocarpaceae are intermediate and similar to Andalau and Mulu. The Lauraceae and Meliaceae have relatively high

Table 7. *The percentage contributions of the principal families, in terms of densities of tree ≥ ca. 30 cm gbh, at the Danum compared with other sites in North-east and East Borneo*

(— indicates < 2.0%, and values in parentheses are families not within the first six at that site. Areas enumerated are given in table 5, with minimum gbh for each study.)

	site						
	Sabah			Brunei and Sarawak		E. Kalimantan	
family	S[a]	SL[a,b]	D[a]	A[a]	M[a]	W[a]	L[a,b]
Euphorbiaceae	10.2	11.9	20.6	10.9	9.0	12.8	18.6
Dipterocarpaceae	27.1	24.0	16.2	16.9	14.7	10.3	6.2
Lauraceae	(2.5)	5.7	6.8	(3.1)	(2.6)	4.8	11.0
Meliaceae	—	5.4	7.5	—	—	(3.0)	4.0
Annonaceae	—	5.9	6.1	(2.4)	—	3.3[c]	8.5
Myrtaceae	6.9	—	5.7	8.0	8.4	—	5.0
Sapotaceae	6.1	(2.0)	(3.6)	—	6.7	5.6	—
Anacardiaceae	5.3	—	—	5.2	(2.6)	—	—
Tiliaceae	4.1	—	(4.4)	—	—	—	—
Myristicaceae	(2.3)	—	—	(5.0)	6.3	3.3[c]	—
Burseraceae	—	—	(2.5)	6.4	4.5[c]	3.7	—
Guttiferae	—	—	—	6.0	4.5[c]	—	—

[a] S, Sepilok (Nicholson 1965); SL, Segaliud-Lokan (Fox 1967); D, Danum (present study); A, Andalau (Ashton 1964); M, Mulu (Proctor *et al.* 1983); W, Wanisaret (Kartawinata *et al.* 1981); L, Lempake (Riswan 1987).
[b] Sepindaceae only at SL (4·6%); Rubiaceae only at L (4·07); both omitted.
[c] Equal sixth ranked

contributions at Danum, but that for Anacardiaceae is low. There is much variation between sites in the contributions made by the remaining families. Danum seems no more aligned with the other Sabah sites than it is with sites outside of Sabah, although it can, at a minimum, be distinguished by the high contributions to density by the Euphorbiaceae and Meliaceae.

Nicholson (1965) provides a complete list of families with the numbers of their trees 12 in (30.5 cm) gbh or more in the 2 ha plot at Sepilok. The rank correlation between this site and Danum is low (20 families with 10 ha^{-1} or more at one site; $r_s = 0.32$, d.f. = 18, $p > 0.05$). The greater overall density of trees at Sepilok than at Danum (table 5) is to a large part accounted for by the former site having over twice the density of dipterocarps (165 ha^{-1} against 76 ha^{-1}). In contrast, at Segaliud-Lokan, Fox (1967) recorded a slightly lower density of dipterocarps than at Danum (68 ha^{-1}). Nicholson (1965) and Fox (1967) both recorded the density of trees in the Dipterocarpaceae

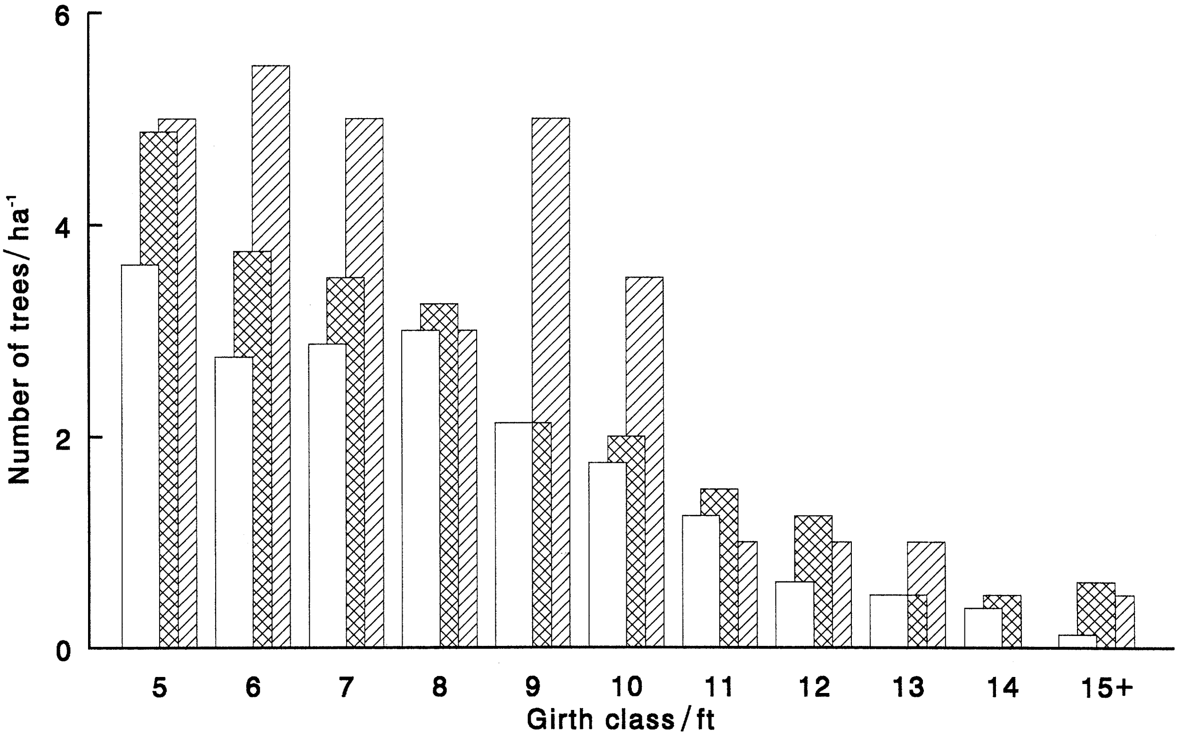

Figure 7. Comparison of the frequency distribution of trees ≥ 5 ft gbh in increasing gbh classes for three sites in Sabah: Danum (open bars), Segaliud-Lokan (cross-hatched bars) and Sepilok (shaded bars).

in 1 ft (30.5 cm) classes from 5 ft gbh. The comparable distribution for the Danum is also closer to Segaliud-Lokan than to Sepilok (figure 7), although it does differ from the former in having fewer trees in the 5–7 ft gbh class. In terms of density, the percentage of trees 240 cm gbh or more which are dipterocarps at Danum is 95% and 88% for plots 1 and 2, respectively, and correspondingly in terms of basal area 97% and 89%. These values fall within the upper end of the range for Sabah (namely 78–98%) given by Whitmore (1984).

7. DISCUSSION

Differences between plots in mean basal area and density of trees in the three size classes are small when judged against the background of variation between sites of this forest type (table 5). Although not statistically, because the sample size is 2 and non-random, some confidence can be placed on the distinctiveness of the Danum with respect to these variables. Because all trees (10 cm gbh or more) were labelled and mapped, the mensuration data are highly accurate. The plots also show a high similarity in species richness, diversity and evenness measures, and in their species–area relations. They may be considered 'close replicates' when species richness particularly is compared with other sites (table 6). A plot area of 4 ha appears to be sufficient at Danum, and ample if only common species are considered. The smooth decline in tree frequency with increasing gbh, fitting a double logarithmic model, does not provide evidence of recent large disturbances to the plots. Overall, the criteria set out have been met and the 8 ha enumerated provides a representative and adequate sample of the forest block.

An unknown error, however, must be attached to species richness and to distributions or indices dependent upon taxonomic identification. That all trees (except those dying during the study) were named twice (and some three times) using both herbarium and field characters lends strong support to a reasonable and acceptable accuracy of determination. With so little fertile material available, it is possible that a few taxa may have been lumped at the initial sorting stage of phase 1 and remained undetected in phase 2. This would decrease the total species count. Equally likely is that several taxa may have been mistakenly split because of the poor botanical specimens, a lack of appreciation of within- against between-species variation in vegetative characters for some taxa and a tendency to separate specimens if there was doubt in allocation. This effect would increase the species count: many of those taxa involved are to 'genus/family only' level and are rarer and less well known. Manokaran *et al.* (1990) at Pasoh similarly used a complement of herbarium and field identification, and on rechecking all trees 10 cm dbh or more in 50 ha 'changed between 5% and 16% of the initial identifications' per hectare subplot. Few other studies in tropical forest have undertaken, or admitted the necessity of, double-checking identifications.

The logseries model is appropriate to tropical forests because it implies that species establish, or go through periods of recruitment, at random time intervals and that a few major environmental factors control patterns in relative abundance (May 1975). The former is supported by the view of randomly located canopy gaps, arising from tree mortalities in time and space, combined with stochastic processes controlling flowering, fruiting and dispersal. The latter recognizes that light probably is the major resource followed by, and interacting with, nutrient supply along local topographic and edaphic gradients. The greater observed frequency of species with only one tree than that predicted by the logseries suggests that forces of local extinction are weak.

A consideration of rareness has led here to a more robust measure in terms of a 'common species richness'. It allows a more operationally feasible definition of minimal area and recognizes the errors in identification attached to rare taxa. In any quantitative analysis at the species level these rare species will have negligible weight.

The paucity of documented studies which meet ecological standards for comparison with Danum is apparent from the literature reviewed here. Comparisons between sites require caution, especially where the plots are small and unreplicated and it is not known how subjectively they were selected: the three sites with plots 1 ha or less in area (table 5), for instance, have the highest recorded basal areas ($>42\ \mathrm{m^2\ ha^{-1}}$). A large plot, or a sample of many small plots over a large area, gives the most reliable results statistically. The soundest comparison for trees 30 cm gbh or more is thus with Segaliud-Lokan (Fox 1967) within Sabah and with Pasoh (Manokaran & LaFrankie 1990) outside Sabah, and on that basis basal area abundance at the Danum is very close to that found in these two similarly extensive studies. (The samples at Andalau (although stratified; Ashton 1964) and Jengka (Poore 1968) are also reliable for large trees.) However, the distinctively low density of trees in Fox's study (table 5) means that even this site may reflect a special environment or history. Only Pasoh provides the scope for comparison down to 10 cm gbh, but at some distance biogeographically. Overall, the Danum has fewer large trees, leading to a relatively lower basal area, when compared with many other dipterocarp forests.

An important feature of the forest at Danum is the low frequency and small size of near-ground canopy gaps. (Possibly the gap count was stochastically lower than average in the years recorded.) Many trees are observed generally to die standing thereby creating small openings into which saplings and poles grow. The seed bank of pioneer trees is low (Kennedy & Swaine, this symposium). In an independent survey of 10 ha of forest at Danum (a 20 m strip along the main west trail) the gap area was estimated at 0.3–0.5% (N. D. Brown, personal communication) which agrees closely with values reported in this study. The high relative density of trees in the Euphorbiaceae, a predominantly understorey family, is an important feature of the forest at Danum, and within that storey exists clear dominance by 2–4 species. This could either be a result of edaphic selection at the site for a few species or, in part, be a reflection of a low level of recent disturbance. Furthermore, fluctuations in the frequencies of trees in 90–160 cm gbh classes could record releases in canopy tree growth caused by abnormally high mortality of emergents on two (or three) occasions in the past. Although this is impossible to date accurately, drought may have been causal; one such event in 1915 in Sabah is well documented (Whitmore 1984). Evidence for fire, despite some findings of soil charcoal (P. Becker, personal communication) remains equivocal.

Campbell (1990) recorded the density of lianas 2 cm gbh or more of all trees 30 cm gbh or more in the two Danum plots. Plots 1 and 2 had 929 ha^{-1} and 833 ha^{-1}, respectively (mean 881 ha^{-1}), and 61% and 54% of the trees carried lianas (mean 57%). Putz & Chai (1987) in lowland dipterocarp forest at Lambir in Sarawak (ten 0.1 ha plots), used a 1 cm minimum dbh and found 391 lianas per ha on trees 10 cm dbh or more. For dipterocarp forest at Mulu, Proctor *et al.* (1983), using the same size classes of tree and liana as Putz & Chai, recorded 440 lianas per ha. Despite the different size threshold the Danum plots appear to have a high density of lianas: this might also be a reflection of the opening of the canopy in the past.

The evidence shown here suggests a hypothesis that the present forest at Danum, at least at this sample location, is at a later stage of recovery from a moderate disturbance some several decades previously. The prediction would be a continuing increase in the density of large trees, basal area and species richness with time. An alternative hypothesis is that the measured attributes of the forest are presently maximal and constant, and this must be explained by special, perhaps edaphic, site conditions. Remeasurement of the enumerated plots can test these ideas, together with an increased knowledge of the area's history and investigations into the nature of the soils.

The Natural Environment Research Council (GR3/5555 and 7171) and the Royal Society South-east Asia Rain Forest Research Committee provided financial support. Permission to conduct research in Sabah was granted by the Danum Valley Management Committee and the Socio-economic Research Unit of Malaysia. We thank E. F. Bruenig for his advice, L. Madani and M. Lantoh for field identifications, and R. Stewart for preparing the figures. This paper is Number A/042 of the Royal Society's South-east Asian Rain Forest Research Programme. J. Aik, K. Kulit and L. Lowa assisted in the field.

REFERENCES

Ashton, P.S. 1964 Ecological studies in the mixed dipterocarp forests of Brunei State. *Oxf. For. Mem.* **25**.

Austin, M.P. & Greig-Smith, P. 1968 The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forest. *J. Ecol.* **56**, 827–844.

Burgess, P.F. 1961 The structure and composition of lowland tropical rain forest in North Borneo. *Malay. Forester* **24**, 66–80.

Campbell, E.J.F. 1990 Ecological relationships between lianas and trees in a lowland tropical rain forest in Sabah, Malaysia. M.Sc. thesis, University of Stirling.

Fox, J.E.D. 1967 An enumeration of lowland dipterocarp forest in Sabah. *Malay. Forester* **30**, 263–279.

Fox, J.E.D. 1973 *Kabili-Sepilok Forest Reserve.* Sabah Forest Record No.9. Borneo Literature Bureau for Sabah Forest Department, Sandakan.

Hill, M.O. 1973 Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**, 427–432.

Ho, C.C., Newbery, D.McC. & Poore, M.E.D. 1987 Forest composition and inferred dynamics in Jengka Forest Reserve, Malaysia. *J. trop. Ecol.* **3**, 25–56.

Kamarudin, I. 1986 Structure and species composition of lowland dipterocarp forest in Danum Valley. B.Sc. thesis, Universiti Kebangsaan Malaysia, Sabah.

Kartawinata, K., Abdulhadi, R. & Partomihardjo, T. 1981 Composition and structure of a lowland dipterocarp forest at Wanariset, East Kalimantan. *Malay. Forester* **44**, 307–406.

Kochummen, K.M., LaFrankie, J.V. & Manokaran, N. 1990 Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *J. trop. For. Sci.* **3**, 1–13.

Magurran, A.E. 1988 *Ecological diversity and its measurement.* London: Croom Helm.

Manokaran, N. & Kochummen, K.M. 1987 Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. trop. Ecol.* **3**, 315–330.

Manokaran, N. & LaFrankie, J.V. 1990 Stand structure of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *J. trop. For. Sci.* **3**, 14–24.

Manokaran, N., LaFrankie, J.V., Kochummen, K.M., Quah, E.S., Klahn, J.E., Ashton, P.S. & Hubbell, S.P. 1990 Methodology for the fifty hectare research plot at Pasoh Forest Reserve. *Forest Research Institute of Malaysia Research Pamphlet* **104**.

May, R.M. 1975 Patterns of species abundance and diversity. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 81–120. Cambridge, Massachusetts: Harvard University Press.

Newbery, D.McC. & Proctor, J. 1984 Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. IV. Associations between tree distribution and soil factors. *J. Ecol.* **72**, 475–493.

Nicholson, D.I. 1965 A study of virgin forest near Sandakan North Borneo. In *Proceedings of the Symposium on ecological research in humid tropics vegetation*, pp. 67–86. Kuching: UNESCO/Government of Sarawak.

Pielou, E.C. 1977 *Mathematical ecology.* New York: J. Wiley & Sons.

Poore, M.E.D. 1964 Integration in the plant community. *J. Ecol.* **52** (Suppl.), 213–226.

Poore, M.E.D. 1968 Studies in Malaysian rain forest. I. The forest on triassic sediments in Jengka Forest Reserve. *J. Ecol.* **56**, 143–196.

Proctor, J., Anderson, J.M., Chai, P. & Vallack, H.W. 1983 Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *J. Ecol.* **71**, 237–260.

Proctor, J., Lee, Y.F., Langley, A.M., Munro, W.R.C. & Nelson, T. 1988 Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *J. Ecol.* **76**, 320–340.

Putz, F.E. & Chai, P. 1987 Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* **75**, 523–531.

Riswan, S. 1987 Structure and floristic composition of a mixed dipterocarp forest, Lempake, East Kalimantan. In *Proceedings of the third round table conference on dipterocarps* (ed. A. Kostermans), pp. 435–458. Samarinda, Indonesia.

Sabah Forest Department. 1987 Biennial report for 1985–86 of Research and Development Division (ed. Y. F. Lee).

Whitmore, T. C. 1984 *Tropical rain forests of the Far East*, 2nd edn. Oxford: Clarendon Press.

Whittaker, R.H. 1970 *Communities and ecosystems*. New York: Macmillan.

Wright, P.S. 1975 *Western parts of Tawau and Ladah Datu districts. The soils of Sabah*, vol. 3. Land Resource study *20*, Ministry of Overseas Development, UK.

Wyatt-Smith, J. 1966 Ecological studies on Malayan forests. *Malayan Forestry Department Research Pamphlet* **52**.