FLORISTIC COMPOSITION AND STAND STRUCTURE OF MIXED DIPTEROCARP AND HEATH FORESTS IN BRUNEI DARUSSALAM

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DAVIES, S.J. & BECKER, P. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. The stand structure and floristic composition of four 0.96-ha plots in mixed dipterocarp (MDF) and tropical heath forests in Brunei are described. All trees ≥5 cm diameter at breast height were mapped, identified and their diameters measured. Soil and root profiles in one MDF and one heath plot are also described. The MDF plot sampled for soil was on a sandstone-derived haplic acrisol with a thick but patchy humus layer. The heath forest plot sampled was on an albic arenosol. Away from large trees, fine and coarse roots were almost absent below 30 cm depth in the heath soil, but present in the MDF soil. Stand basal area was slightly lower in the two heath plots than the two MDF plots, whereas stem densities were not consistently different between the formations. Stand density and basal area were highest on upper land at both MDF plots and one heath plot, but were highest in a swampy area in the other heath plot. The MDF plots had higher species richness and lower species dominance than the heath plots. The MDF and heath plots were floristically distinct. *Dryobalanops aromatica* contributed most to basal area in both MDF plots. *Agathis borneensis* accounted for 65% of basal area and 16% of trees at one of the heath plots. *Gluta beccarii* contributed 11% of basal area at the other heath plot. The Euphorbiaceae and Burseraceae contributed relatively more to species richness, tree abundance and basal area in the MDF plots than in the heath plots. The Myrtaceae contributed relatively more to species richness, tree abundance and basal area in the heath plots. The Araucariaceae were unique to the heath plots, and the Clusiaceae and Sapotaceae contributed relatively more to species richness in the heath plots. The plots were compared with other MDF and heath plots in Borneo. The heath plots were typical of the coastal heath forest growing on medium-deep white sands in northwest Borneo. The MDF plots were similar to other very species-rich MDF from northwest Borneo growing on sandstone-derived soils with moderate to high sand content.

Key words: Tropical rain forest - heath forest - mixed dipterocarp forest - Borneo - species richness - size class distribution - density - basal area

DAVIES, S.J. & BECKER, P. 1996. Kandungan flora dan struktur dirian hutan dipterokap dan hutan rawa di Brunei Darussalam. Struktur dirian dan kandungan flora empat plot 0.96 ha di hutan dipterokap campur (MDF) dan hutan rawa tropika di Brunei dibincangkan. Semua pokok dengan diameter aras dada ≥ 5cm telah dipetakan, dikenalpasti dan diameternya diukur. Tanah dan profil akar di dalam satu plot MDF dan satu plot hutan rawa juga dibincangkan. Plot MDF dimana tanahnya disampel adalah batu pasir berjenis akrisol haplik dengan lapisan humus yang tebal

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tetapi bertompok-tompok. Plot hutan rawa yang disampel adalah pada albik arenosol. Jauh daripada pokok-pokok besar, akar-akar halus dan kasar hampir-hampir tidak wujud pada kedalaman 30 cm di dalam tanah rawa, tetapi wujud di dalam tanih MDF. Luas pangkal dirian adalah lebih rendah di dalam dua plot hutan rawa berbanding dengan plot MDF, manakala ketumpatan batang tidak berbeza dengan konsisten di antara pembentukan. Ketumpatan dirian dan luas pangkal adalah paling tinggi pada tanah yang lebih tinggi di kedua-dua plot MDF dan satu plot rawa, tetapi tertinggi di kawasan berpaya di plot rawa yang lain. Plot-plot MDF mempunyai spesies yang lebih kaya dan kurang dominan daripada plot-plot rawa. Plot-plot MDF dan rawa adalah jelas berflora. *Dryobalanops aromatica* menyumbangkan paling banyak kepada luas pangkal di dalam kedua-dua plot MDF. *Agathis borneensis* memenuhi 65% luas pangkal dan 16% daripada pokok-pokok di salah satu plot rawa. *Gluta beccarii* menyumbangkan 11% daripada luas pangkal di plot rawa yang lain. Euphorbiaceae dan Burseraceae banyak menyumbang kepada kekayaan spesies, kepadatan pokok dan luas pangkal di dalam plot MDF berbanding dengan plot rawa. Araucariaceae adalah unik kepada plot rawa, dan Clusiaceae dan Sapotaceae menyumbangkan lebih banyak kepada kekayaan spesies di plot rawa. Plot-plot rawa adalah tipikal kepada hutan rawa pesisiran pantai yang tumbuh di pasir putih yang sederhana-dalam di Barat-Laut Borneo. Plot-plot MDF ini adalah sama dengan MDF lain yang sangat kaya-spesies dari Barat Laut Borneo yang tumbuh di atas tanah berjenis batu pasir dengan kandungan pasir yang sederhana hingga tinggi.

Introduction

The lowland tropical rain forests of Borneo are among the most diverse plant communities on earth (Phillips *et al.* 1994). The stand structure and floristic composition of these forests are spatially variable with respect to altitude, soils, parent material, drainage, and the predominant disturbance regimes. A major challenge for tropical ecologists is to gain a mechanistic understanding of the factors that influence the variation in structure and composition of these forests.

In Borneo, two of the major lowland forest formations are mixed dipterocarp forest (hereafter MDF) and heath (or kerangas) forest (see for example, Richards 1936, Ashton 1964, Brunig 1974, Whitmore 1984). MDF is the most widespread of the lowland forest formations in Borneo, occurring on a wide range of sites. Characterised by a very tall (40-60 m) canopy typically dominated by a mixed species association of Dipterocarpaceae, the structure of the MDF is spatially variable (Ashton & Hall 1992). The soils of MDFs vary enormously, being derived from a variety of parent materials, including sandstone, shale, basalt and granite. Heath forest occurs on base poor, acidic, podsolised soils usually derived from sand or sandstone (Whitmore 1984). The general features of heath forest such as leaf sclerophylly, the thick and spongy humus layer, high understorey light levels, a general lack of large climbers, and the peculiar floristic composition have been qualitatively well described (Richards 1936, Browne 1952, Ashton 1971, Brunig 1974, Whitmore 1984). The physiognomic and floristic distinctiveness of heath forest has led to considerable debate as to the abiotic factors that control these features (Whitmore 1984). Both drought stress (Brunig 1970) and nutrient deficiency (Proctor *et al.* 1983a) have been proposed as potential mechanisms.

This paper describes the structure and floristics of four 0.96-ha samples of lowland tropical rain forest in Brunei Darussalam. Two of the forests are MDF and two are heath forest. These plots form the research sites for an on-going project designed to examine possible mechanistic bases for the distribution of these forest formations. Detailed studies of nutrient dynamics and water relations of MDF and heath forest are being carried out (Barker & Becker 1995, Becker 1995, Becker & Barker 1995). For the purpose of evaluating the generality of these experimental studies, it is important that the chosen forests are representative of their respective formations. After describing the structure and floristics of the four plots, they are compared with other MDFs and heath forests in Borneo.

Materials and methods

Site description

MDF and heath forest are well-represented forest formations in Brunei. Two MDFs and two heath forests were chosen for study. Details of the four plots are provided in Table 1, their locations shown in Figure 1, and their topographies shown in Figure 2. Throughout this paper we use the soil nomenclature of FAO-UNESCO-ISRIC (1988), except when citing other research, in which case we provide the nearest FAO equivalent in parentheses.

Table 1. Forest type, number of species and families, tree density, basal area, species dominance*, and the number of species in the first 500 trees (SPP500+) for all trees ≥5, ≥10 and ≥30 cm dbh in two mixed dipterocarp and two heath forest plots in Brunei Darussalam

Plot	Forest type	Species	Families	Density (ha^{-1})	Basal area (m^2 ha^{-1})	Dominance*	SPP500
Trees ≥ 5 cm dbh							
Andulau	MDF	393	52	1484	38.6	0.021	236
Ladan	MDF	298	47	1079	42.5	0.034	196
Badas	Heath	113	40	1341	35.7	0.213	76
Sawat	Heath	171	48	1613	36.6	0.061	132
Trees ≥ 10 cm dbh							
Andulau	MDF	256	43	596	35.2	0.023	235
Ladan	MDF	194	43	480	40.2	0.052	195
Badas	Heath	77	31	551	32.7	0.309	74
Sawat	Heath	121	39	705	33.1	0.082	114
Trees ≥ 30 cm dbh							
Andulau	MDF	58	24	89	24.1	0.079	-
Ladan	MDF	61	19	116	31.5	0.078	-
Badas	Heath	16	9	97	22.7	0.753	-
Sawat	Heath	38	15	129	19.6	0.147	-

* Dominance = N_d/N_t, where N_d = number of individuals in the most abundant species, and N_t = total number of individuals (May 1975).

+ Species richness between sites should be compared after taking tree densities into account (Phillips *et al.* 1994). SPP500 is the number of species in the first 500 trees.

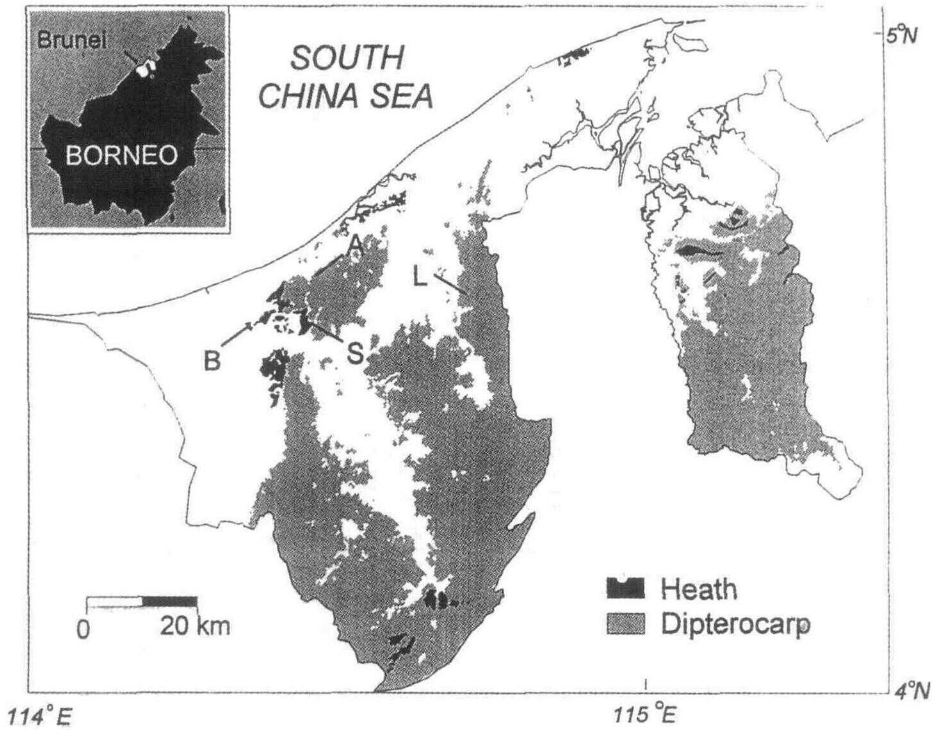

Figure 1. Map showing the locations of the study plots in Brunei Darussalam. MDF: A = Andulau, L = Ladan. Heath forest: B = Badas, S = Sawat. Based on Anderson & Marsden (Forestry Consultants) Ltd. (1984)

Mixed dipterocarp forest

Andulau Forest Reserve (F.R.) comprises an area of 12 400 ha, most of which was selectively logged during the 1950s to early 90s. The forest and soils in the still unlogged Research Compartments 7 and 8 (300 ha)were studied extensively by Ashton (1964). Our plot (Andulau), 4 km southeast of Sungai Liang (4° 39' 26" N, 114° 30' 57" E, elevation 37-59 m), was located in unlogged forest just north of his plots 43 and 44 and included his plot 6. The topograhy is undulating over soft interlaminated clay and sandstone of the Liang formation. The soils in the plot grade from yellow podsolic soils (sandy-textured haplic acrisols, henceforth sandy haplic acrisols for brevity) on the hills to somewhat hydromorphic alluvial soils (probably dystric fluvisols) in the valley (Ashton 1964).

The Ladan Hills plot (Ladan) is located in Compartment 57 of Ladan Hills F.R. (34 000 ha), 9 km southeast of Kampong Lamunin (4° 37'15"N, 114° 44'39"E, elevation 39-72 m). Surrounding areas have been logged, but the plot is unlogged. Located on the western slope of an anticline formed from the Belait formation, the soils are relatively clay-rich heavy textured haplic acrisols derived from interbedded sandstone and shale.

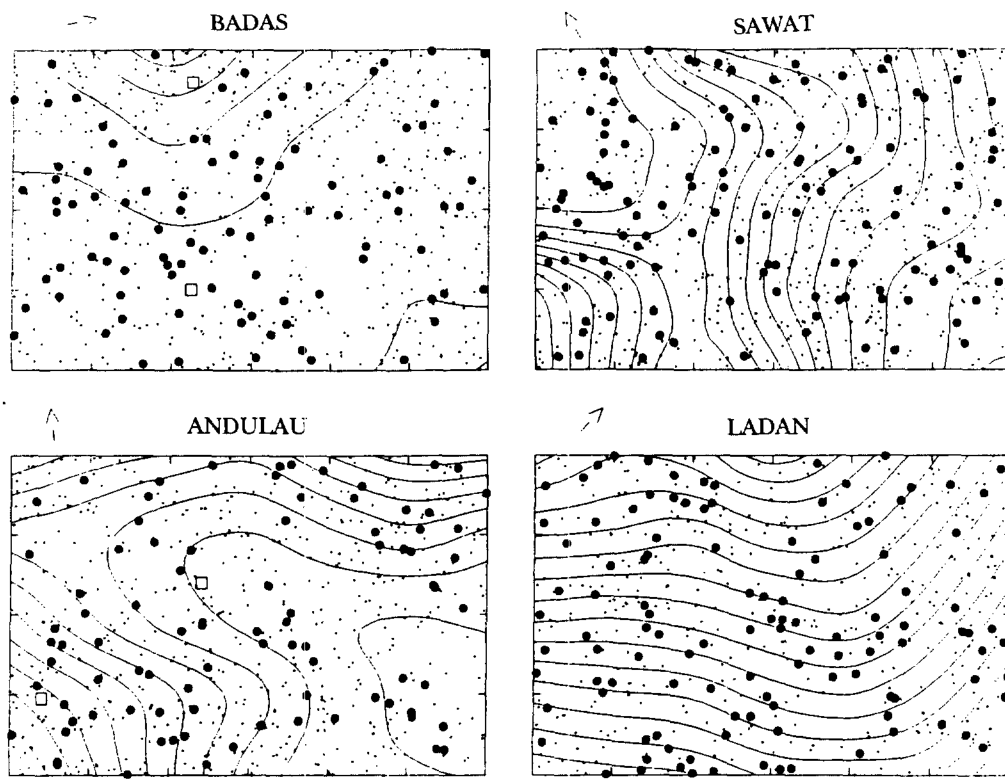

Figure 2. Spatial distribution of trees in four 0.96-ha plots (small dots 10-30 cm dbh trees, large dots ≥30 cm dbh trees). Contour lines show 2-m intervals of elevation at Andulau and Ladan and 1-m intervals at Badas and Sawat. The arrows at upper left show true north. Soil pits at Andulau and Badas are indicated by squares

Heath forest

Badas F.R. is 14 km southwest of Sungai Liang (4° 34'05"N, 114° 24' 53"E, elevation 11-16 m). Badas F.R. comprises 73 ha, 10% of which was destroyed by fire following a severe drought in 1992 (Becker & Wong 1992). The plot (Badas) is located in unlogged forest (GP 302 Lot 3661) c. 200 m from the nearest fire damage. The plot is on a Pleistocene terrace, a deep white sand albic arenosol with little topographic relief.

The plot (Sawat) in Bukit Sawat Research Forest (GP 793 Lot 5651), 11 km south of Sungai Liang (4°34'37"N, 114°30'11"E', elevation 11-23 m), is also on a Pleistocene terrace with humic podzols. There is considerably more topographic relief than at Badas, and areas of impeded drainage are quite common. The research forest was selectively logged in the late 1960s; however, there are no stumps in the plot, so we cannot be certain that it was logged. The stand structure resembles that at Badas, except for the absence of emergent *Agathis borneensis*. Bukit Sawat Research Forest had lower densities of this species than Badas Forest Reserve even prior to logging (P.S. Ashton, pers. comm.).

Climate

The nearest station with long term meteorological records is Sungai Liang Agricultural Station for Andulau, Badas and Sawat, and Kilanas Agricultural Station for Ladan. Both stations have similar average annual rainfall totals of c. 3000 mm with less rainy periods during February-March and July-September (Becker 1992, Cooper 1992). Median rainfall during 1960-89 exceeded 100 mm in every month except February at Kilanas, but such averages conceal the frequent occurrence of droughts. Periods when the sliding thirty-day total of rainfall remained less than 100 mm for more than a month have occurred about once every two years. The exceptionally severe drought of 1992 caused substantial mortality of understorey trees (1-5 cm dbh) in the heath forest at Badas, but not in the heath forest at Sawat or the MDF at either Andulau or Ladan (Becker & Wong 1993).

Atmospheric temperatures are typical for the region with high even temperatures (mean daily maxima = 32.1 °C and mean daily minima = 24.1 °C) without substantial seasonal fluctuations (unpublished data for Sungai Liang Agricultural Station, 1983-1992, Brunei Meteorological Service).

Methods

Plot establishment and floristic survey

Plots were sited close to access tracks but away from other research projects with their attendant foot traffic. An effort was made to include topographic variation, but swampy areas and large gaps were avoided, with the exception of a swampy area in the Sawat plot. The proportions of different topographic classes in the plots may not be representative for the sites. Rectangular plots (80 × 120 m, 0.96 ha) were selected because this shape fit best within existing tracks at the four sites. The plots were laid out by a commercial surveyor and gridded in a horizontal plane with aluminium stakes at every 10 m (Truebridge Callender Beach 1992).

All self-supporting woody plants ≥ 5 cm diameter at breast height (dbh) were tagged, mapped, measured, and identified, generally following the procedures of Manokaran *et al.* (1990). Numbered aluminium tags were nailed to trees ≥10 cm dbh (20 cm below the point of measurement) or tied with a slip knot to smaller trees using fishing line. Diameter was measured to 1 mm with a fabric tape at 1.3 m above the ground on the upslope side or 20 cm above the apex of the tallest buttress after removing loose bark and moss. The point of measurement was painted red. Approximate dates of measurement in 1992 were: Badas 7-31 July, Andulau 1-15 August, Sawat 16 August - 7 September, Ladan 21 September - 15 October. All trees within two randomly selected 10 × 10 m subquadrats in each plot were remeasured and found to agree within 2 mm. Trees were mapped to 0.1 m by measuring the distance and direction from the centre of their base to a grid marker and converting to rectangular coordinates. The adult life-form of species was classified as either emergent tree (>60 cm dbh and > 30 m tall), canopy tree (30-60 cm dbh and 20-30 m tall), understorey tree (10-30 cm dbh and 10-20 m tall), or treelet (≤10 cm dbh and ≤10 m tall) (Kochummen *et al.* 1991).

Unless an immediate and certain identification could be made, a small sample (usually a twig with a few leaves and fertile material when available) was taken from each tree. For common but unrecognised species, only the first few individuals were sampled. Morphologically variable species and taxonomically difficult groups were always collected. Overall, 50-80% of trees were collected by professional tree climbers, a pruner, or slingshot, with notes sometimes made on bole and slash characteristics. Dried specimens were sorted to morphospecies, which were then identified as far as possible with reference to Brunei (BRUN) and Kuching (SAR) herbaria. Identifications were usually to specific, occasionally to subspecific level. Nomenclature mostly follows Whitmore (1972, 1973), Ng (1978, 1989), and Anderson (1980). Herbarium sheets (stamped "UBD Forest Research Plots - Voucher Specimen") were prepared for samples of each morphospecies, with at least one sample from each plot in which the species occurred. These specimens were deposited in the herbarium of the Biology Department of Universiti Brunei Darussalam. Printed and electronic copies of the plot raw data were deposited with the Brunei Forestry Department and the Biology Department of Universiti Brunei Darussalam. Requests for copies of the data should be made in writing to the Head of Biology at the University.

In the four plots 716 taxa were identified: 566 (79.1%) taxa were identified to species or subspecies, 131 taxa (18.3%) were determined to genus only, 15 taxa (2.1%) were determined to family only, and 4 taxa (0.6%) remained unidentified. On an individual stem basis 94.4% (5206 of 5517 individuals in the four plots) were identified to species or subspecies, and 99.5% of individuals were determined to genus. For the purposes of this analysis, all identified taxa (i.e. species and subspecies) are referred to as species. Specimens identified only to genus or family were each counted as a separate genus or family respectively; for example, the 4 taxa unidentified at the family level were considered to be from different families.

Two methods were used to compare floristic similarity between plots. Jaccard's coefficient (J) was used to compare similarity in the presence/absence of species between plots [$J = c/(a + b - c)$, where c is the number of species in common between a pair of plots, and a and b are the total number of species in each plot, Krebs (1989)]. To compare the floristic similarity between plots taking species abundance or basal area into account, Horn's modification (C_H) of Morisita's Index (Krebs 1989) was used [$C_H = (2 \Sigma X_{ij} X_{ik}) / \{[(\Sigma X_{ij}^2/N_j^2) + (\Sigma X_{ik}^2/N_k^2)] N_j N_k\}$, where X_{ij} and X_{ik} are the number of individuals (or basal area) of species i in plots j and k, and N_j and N_k are the total number of individuals (or basal area) in plots j and k]. Both indices can potentially vary between 0 and 1, with larger numbers indicating greater similarity between plots.

Soil pits and root profiles

Soil pits were excavated in one MDF plot (Andulau) and one heath plot (Badas) to assess general differences between the soils. Pits were deliberately sited at some distance from large trees to avoid the overriding influence of their large roots. Two pits (c. 1.2 m long × 0.6 m wide × 1.2 m deep) were dug in each plot in July 1993 (Figure 2), and the freshly cleaned upslope pit faces were described within two weeks. Color was designated according to Munsell soil color charts (Anonymous 1990), and texture according to Leamy and Panton (1966).

Roots were sampled from 10-cm thick strata to a depth of 1 m on three faces of each soil pit. A soil block with roots was collected by driving a U-shaped metal sheet (10 cm high × 20 cm long × 10 cm deep) into the pit face and then cutting the block free. Roots were removed by hand, but when fine roots were especially abundant in humus layers they were separated by wet sieving (1.7 mm mesh). Roots were frozen until processing three weeks later. Below 40 cm depth, pairs of adjacent 10-cm strata were combined for analysis as root quantities were small. At the soil pit in the topographic depression at Badas, an indurated humic horizon (hard-pan) precluded sampling below 60 cm depth. The lengths of fine roots (≤ 2 mm in diameter) were quantified according to Tennant (1975) after discarding obviously dead roots. Weights of fine and coarse roots were determined after oven drying to a constant weight at 105 °C.

Results

Soil descriptions

Andulau Pit 1

At the middle of steep (20° slope) hillside. Nearest large (>30 cm dbh) tree 4 m away. Medium density of sapling undergrowth. Ashton's (1964) yellow podsolic soils (sandy haplic acrisol).

5 - 0 cm	Uniform litter of coriaceous leaves.
0 - 10 cm	Dark reddish brown (5YR 3/2), loosely matted raw humus admixed with sand. High density of mostly horizontal, twiggy roots.
10 - 15 cm	Light yellowish brown (10YR 6/4) sand. Roots abundant.
15 - 55 cm	Brownish yellow (10YR 6/6) loamy sand. Roots common.
55 - 140 + cm	Reddish yellow (7.5YR 6/8) sandy loam with occasional greyish mottled patches (5-10 cm). Roots uncommon. Occasional soil charcoal at 80 - 90 cm depth.

Andulau Pit 2

Between center and margin of upper end of broad valley on slightly sloping (3°) ground. Nearest large tree 4 m away; sparse undergrowth. During very rainy periods there is surface wash and standing water in this area (Ruslan Kurus, pers. comm.). Probably intermediate between Ashton's (1964) well- and badly-drained alluvial soils (probably dystric fluvisol of mixed texture).

3 - 0 cm	Uniform litter of coriaceous leaves.
0 - 5 cm	Dark reddish brown (10YR 5/6), humus stained sand. Moderately rooted.
10 - 26 cm	Light yellowish brown (2.5Y 6/4) loamy sand with pronounced greyish mottling. Few roots.
26 - 75 cm	Reddish yellow (7.5YR 6/6) sticky sandy clay.
75 - 92 cm	Pale yellow (2.5Y 7/3) grading to whitish sand, strongly mottled. No roots.
92 - 115 + cm	Light yellowish brown (2.5Y 6/3) clay commencing just above water table at 101 cm. No roots.

Badas Pit 3

On level (1°) ground of terrace. Nearest large tree 4 m away. Dense sapling undergrowth. Ashton's (1964) leached white sands (albic arenosol).

3 - 0 cm	Uniform litter of coriaceous leaves.
0 - 3 cm	Dark reddish brown (5YR 2.5/2) matted raw humus with some white sand grains. Very densely rooted by fine roots.
3 - 14 cm	Dark reddish brown (5YR 2.5/2) finer humus with some white sand. Abundantly rooted by somewhat larger roots than in upper layer.
14 - 25 cm	Dark brown (7.5YR 4/2) humus stained sand. Roots common.
25 - 125 + cm	White sand. Occasional sinker and horizontal roots. Humus stained sand commenced at 180 cm and indurated humic horizon at 210 cm as determined by auguring.

Badas Pit 4

Midslope in shallow depression (9° slope). Nearest large tree 5 m away. Medium sapling density. Poorly drained gleyic podsol. The boundaries of layers below 10 cm depth were variable and seemed to follow irregularities in the surface of the indurated humic horizon, so average depths were noted.

3 - 0 cm	Uniform litter with coriaceous leaves and abundant palm frond fragments.
0 - 4 cm	Black (5YR 2.5/1) mat of humus with some white sand. Densely rooted.
4 - 10 cm	Dark reddish brown (5YR 2.5/2) humus with some sand. Abundantly rooted.
10 - 31 cm	Dark reddish brown (5YR 3/2), strongly humus stained sand. Roots common.

31 - 53 cm	Pinkish grey (7.5YR 6.2), less uniformly stained sand with a few areas of grey sand. Staining sometimes concentrated in a series of fine humic bands. Roots uncommon. Substantial amount of large pieces of soil charcoal.
53 - 65 cm	Dark reddish brown (5YR 2.5/2) humus-stained sand lying just above indurated humic horizon with wet surface. A few roots proliferated just above hard-pan.

Root profiles

Roots were markedly concentrated in the upper 10-20 cm of the soil at both Andulau and Badas (Figure 3). Spatial heterogeneity of root density was very high as indicated by high between-sample variance. Nevertheless, the following generalisations are thought likely to hold. Fine and coarse roots were nearly absent at Badas below 30 cm depth but many were still present at Andulau. This does not mean that individual trees at Badas are all shallowly rooted. Tap roots there frequently exceed 1 m depth (Becker & Wong 1992), and as noted above, soil pits were sited away from large trees. Coarse roots were much more concentrated in the upper 10 cm of soil at Badas compared with Andulau, and this likely accounts in part for the vulnerability of heath vegetation to forest fire (Becker & Wong 1992). There is probably no great distinction between Andulau and Badas in the density of fine roots in the upper 10 cm of soil, despite appearances in Figure 3. If a single extremely high value for Pit 1 (Andulau) is excluded, mean fine root length drops from 15 400 to 8900 m m^{-3}, compared with 7900 m m^{-3} for Pit 3 (Badas). A *caveat* is that the comparison probably has to be restricted to areas of Andulau that have thick humus. There is strong spatial variation in humus depth in MDF on sandstone-derived soils, and probably there is associated variation in fine root density (P. Becker, pers. obs.). The root density profile did not appear to be much affected by topography (making allowance for the high variance in fine root distribution) and the associated hydrological effects on the soil profile (see soil descriptions above), except that coarse roots were greatly reduced at the valley site compared with the midslope site at Andulau.

Species richness

In total 716 species ≥ 5 cm dbh occurred in the four plots, consisting of 70 families and 224 genera. There was a considerable range in the species diversity among the plots, with the richest plot (Andulau, MDF) having 393 species, more than three times as many species as the floristically poorest plot (Badas, heath) with 113 species (Table 1). The other two plots had 298 (Ladan, MDF) and 171 (Sawat, heath) species. The 716 species found in just under 4 ha represent approximately 25% of the estimated tree flora of Brunei (P .S. Ashton, pers. comm.).

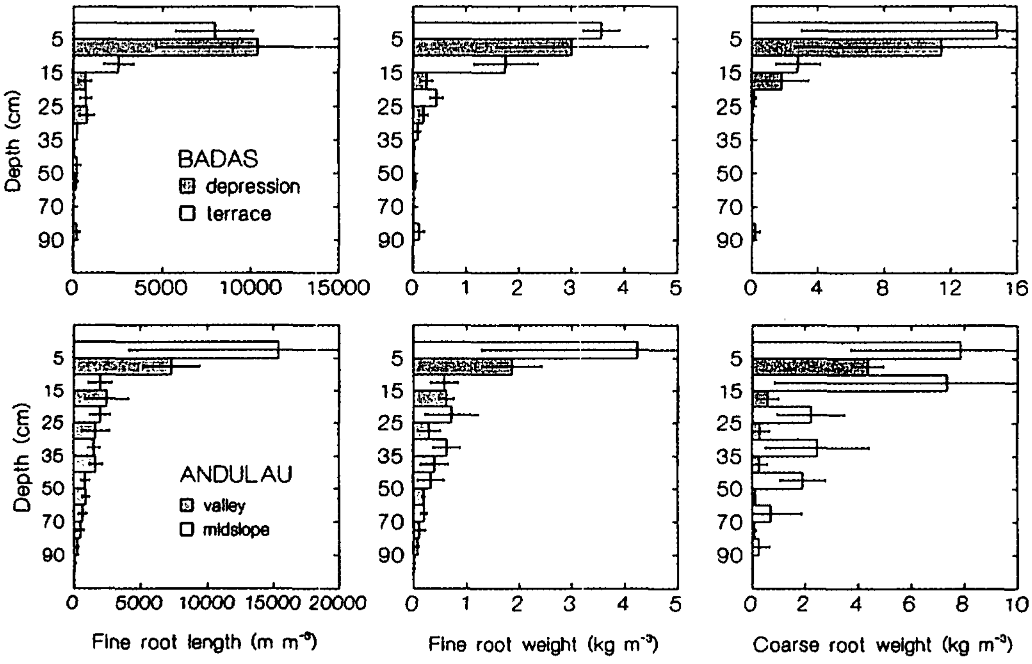

Figure 3. Root densities (mean and s.d., n = 3) in two soil pits at both Andulau and Badas. The depth labels are for the midpoint of 10- or 20-cm thick strata. There were no samples collected below 60 cm depth at Pit 4 (Badas depression).

The MDF plots were significantly more species-rich than the heath plots (Table 1). This is not simply due to differences in stand density among the plots, as the number of species in the first 500 trees (SPP500, see Table 1 and Phillips *et al.* 1994) was considerably higher in the MDF plots. Between the MDF plots alone, there were almost 100 more species in Andulau than in Ladan; this was partly due to a higher stem density in Andulau, but Andulau was still considerably more rich when SPP500 values were compared (Table 1). For the heath plots, Sawat had 171 species and Badas had 113 species. The SPP500 value was also higher at Sawat than Badas indicating a higher species richness at Sawat. This may be partly attributed to the higher dominance of common species at Badas (Table 1, see below). Also, Sawat is far more topographically heterogeneous than Badas, and may provide microhabitat variation suitable for a wider range of species (see analysis below).

Floristic composition

The more important species in terms of basal area and stem abundance for each of the plots are listed in Table 2. The forest at Badas is strongly dominated by the emergent tree *Agathis borneensis* which contributes 64.5% (23.1 $m^2 ha^{-1}$) of the basal area and 16.2% (217) of the trees ≥ 5 cm dbh (Table 2). The most dominant subcanopy tree was the nanophyllous *Eugenia bankensis* with 21.3% (285) of the trees. Other important species at Badas include *Canarium caudatum* (Burseraceae), and *Cotylelobium burckii* (Dipterocarpaceae). Below 5 cm dbh there is quite a rich ground flora and dense shrub layer with very high densities of *Agrostistachys longifolia* (Euphorbiaceae) which rarely exceeds 5 cm dbh at this site.

The vegetation in the other three plots is not strongly dominated by any species (Table 1). In the other heath plot, Sawat, large individuals of *Gluta beccarii* are relatively abundant in the swampy corner of the plot, contributing 11.3% (4.1 $m^2 ha^{-1}$) of basal area. *Dipterocarpus borneensis* is the most abundant species with 6.1% of stems and 6.8% (2.5 $m^2 ha^{-1}$) of basal area. The understorey varies across the topographic gradient; however, *Nepenthes ampullaria* is quite abundant as a ground cover.

The MDF plots show even less tendency towards species dominance (Table 1). This is at least partly due to the small size of the plots and the extremely high species richness. A small number of very large trees of the emergent dipterocarp, *Dryobalanops aromatica,* contribute most to basal area in both MDF plots, 13.3% (5.6 $m^2 ha^{-1}$) at Ladan and 7.5% (2.9 $m^2 ha^{-1}$) at Andulau (Table 2). Other important species at Ladan include *Allantospermum borneensis* and *Dipterocarpus conformis.* At Andulau other important canopy species include *Shorea mecistopteryx* and *Shorea faguetiana* (Table 2).

Community similarity

Species

As expected, the floristic composition of the two MDF plots and the two heath plots were more similar to each other than any plot was to a plot of a different forest type (Table 3). The two heath plots had 80 species in common (Jaccard's coefficient of similarity, J = 0.39). The two MDF plots had 137 species in common (J = 0.25). The four possible MDF-heath forest comparisons had a range of 14 - 21 species in common and a floristic similarity, J, of only 0.03-0.04. Using species presence-absence data there was no obvious difference in similarity between any particular pair of plots from the different forest types (Table 3). Incorporating stem abundance and basal area into estimates of plot similarity demonstrated that the heath plot at Badas was less similar to the MDF plots than Sawat was. This is largely due to the dominance of *Agathis* and the low species richness at Badas. Horn's Index also showed the two heath plots to be more similar to each other than the MDF plots were to each other (Table 3).

Table 2. Important species for two MDF and two heath forest plots in Brunei Darussalam by tree stature class. The three major contributors to basal area and abundance for each plot and stature class are listed. Basal area (ba%) and stem number (n%) are listed as percentage contributions for trees ≥ 5 cm dbh for each plot.

		Mixed dipterocarp forest			
Andulau			Ladan		
		Emergent and canopy trees			
	ba%	n%		ba%	n%
Dryobalanops aromatica	7.5	1.6	*Dryonalanops aromatica*	13.3	1.0
Koompassia malaccensis	5.9	0.2	*Dipterocarpus conformis*	5.6	0.4
Shorea mecistopteryx	5.5	1.5	*Shorea virescens*	3.9	0.2
Shorea faguetiana	5.4	1.6	*Allantospermum borneensis*	2.9	3.4
Lophopetalum subobovatum	1.6	1.4	*Shorea biawak*	2.3	2.3
Horsfieldia polyspherula	0.4	1.3	*Vatica micrantha*	0.6	1.9
		Understorey trees and treelets			
	ba%	n%		ba%	n%
Parastemon spicatum	0.8	0.1	*Mangifera blommesteinii*	1.1	0.3
Xanthophyllum ferrugineum	0.7	1.2	*Pentace* sp.	0.9	2.5
Garcinia brevipes	0.7	0.5	*Hydnocarpus* cf. *subfalcata*	0.8	1.8
Mallotus wrayi	0.4	2.1	*Lophopetalum glabrum*	0.4	2.8
Diospyros brachiata	0.6	1.3	*Mallotus wrayi*	0.3	2.5
Polyalthia canangioides	0.2	1.2	*Koilodepas longifolium*	0.3	1.9
		Heath forest			
Badas			Sawat		
		Emergent and canopy trees			
	ba%	n%		ba%	n%
Agathis borneensis	64.5	16.2	*Gluta beccarii*	11.3	2.7
Cotylelobium burckii	5.4	4.8	*Dipterocarpus borneensis*	6.8	6.1
Heritiera albiflora	1.4	1.1	*Shorea pachyplylla*	6.2	0.7
Canarium caudatum	0.9	5.7	*Shorea multiflora*	3.3	3.6
Aglaia glabrata	1.0	4.3	*Copaifera palustris*	3.0	3.4
Eugenia muelleri	1.1	3.9	*Calophyllum ferrugineum*	2.0	3.2
		Understorey trees and treelets			
	ba%	n%		ba%	n%
Eugenia bankensis	4.9	21.3	*Eugenia* cf. *ampullaria*	1.3	0.9
Nephelium lappaceum	1.4	4.0	*Garcinia dryobalanoides*	0.6	1.7
Eugenia cf. *ampullaria*	0.6	0.7	*Ternstroemia aneura*	0.4	1.7
Actinodaphne borneensis	0.6	4.3	*Cleistanthus gracilis*	0.4	1.5
Garcinia dryobalanoides	0.5	2.1	*Diospyros hermaphroditica*	0.4	1.1
Eugenia kuchingensis	0.3	1.1	*Baccaurea bracteata*	0.3	1.1

Table 3. The number of species in common and estimates of floristic similarity among four plots in MDF and heath forest in Brunei Darussalam. *J* refers to Jaccard's coefficient of similarity based on presence/absence of species. C_{Hn} and C_{Hba} are Horn's Indices of floristic similarity which incorporate species abundance (n) and species basal area (ba) respectively.

	Number of species in common	*J*	C_{Hn}	C_{Hba}
Within heath forest				
Badas vs. Sawat	80	0.39	0.257	0.105
Within MDF				
Andulau vs. Ladan	137	0.25	0.159	0.026
Between heath forest & MDF				
Badas vs. Andulau	17	0.03	0.002	2.6×10^{-5}
Badas vs. Ladan	14	0.04	0.0003	1.2×10^{-6}
Sawat vs. Andulau	21	0.04	0.039	0.009
Sawat vs. Ladan	20	0.04	0.005	0.001

Only four species *(Bhesa paniculata, Dacryodes incurvata, Alseodaphne insignis* and *Koompassia malaccensis)* occurred in all four plots. These species are well known to be widespread throughout the west of Borneo (Anderson 1980), and Hall (1991) found the first two of these species in three forests in Sarawak representing a wide range of MDF types. Twenty-two species (3.1%) occurred in three or more plots. Among these the Dipterocarpaceae were represented by only one species *(Cotylelobium melanoxylon),* a somewhat lower representation than might be expected (given that the Dipterocarpaceae contribute 9% to overall species diversity). This may suggest strong site specificity of dipterocarp species, as Ashton (1964) maintains (Tables 3 & 7).

When individuals of the 42 species occurring in both MDF and heath forest were mapped in each of the plots (Figure 4), there was no obvious indication of micro-habitat preference for these widespread species, such as toward gullies or ridges. The possible exceptions to this were at Badas where there appeared to be a higher density of widespread larger trees in the depression in the west of the plot, and at Sawat where there appeared to be fewer widespread individuals in the swampy northern corner of the plot.

Families and genera

In terms of contribution to species diversity by family at each of the plots, there were some clear differences between the MDF and the heath plots (Table 4). The MDF plots had far higher numbers of species per family overall, so the percentage contribution and ranked contribution of families were compared. The Euphorbiaceae, Burseraceae and Rubiaceae had higher relative species richness in the MDF plots than in the heath plots in this study, whereas the Myrtaceae, Clusiaceae and Sapotaceae were relatively more species-rich in the heath plots. A number of other families showed no obvious trends (Table 4). The relatively low diversity of Dipterocarpaceae at Andulau was notable, although the absolute number of species was still very high. *Eugenia*, *Diospyros* and *Shorea* were among the five most speciose genera in all four plots. The most notable differences between forest types in the speciose genera were that *Calophyllum* was more speciose in the heath plots than in the MDF, and *Xanthophyllum* was more speciose in the MDF plots.

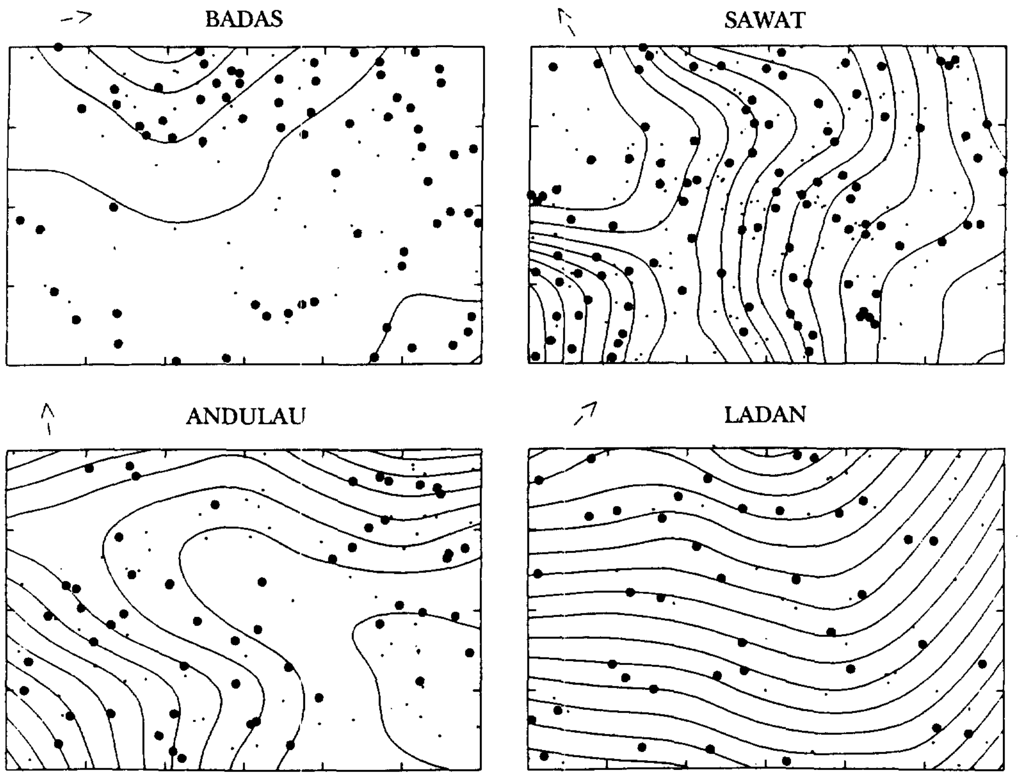

Figure 4. Spatial distribution of all individuals (5-10 cm dbh, small dots; ≥ 0 cm dbh, large dots) of species occurring in each plot that also occur in a plot from a different forest type. Other conventions as in Figure 2.

Basal area and abundance

In terms of basal area and stem abundance the contribution of families also differed among the plots and between the forest types (Table 5). The data are presented as percentage contribution and ranked contribution to account for among-plot variation in basal area and abundance. The ranking of families did not vary substantially when different size classes (≥5, ≥10, or ≥30 cm dbh) were

Table 4. Contribution of families to species richness in two MDF and two heath forest plots in Brunei Darussalam for trees ≥ 5 cm dbh with respect to number (n) of species per family, percentage (%) of total species in each plot, and rank of family (Rank) in species richness contribution for each plot. Families are grouped according to forest types in which they have relatively greater species richness.

	Mixed dipterocarp forest						Heath forest					
	Andulau			Ladan			Badas			Sawat		
	n	%	Rank	n	%	Rank	n	%	Rank	n	%	Rank
MDF > heath forest												
Euphorbiaceae	36	(9.2)	1	30	(10.1)	1	8	(7.1)	3	15	(8.8)	2
Burseraceae	20	(5.1)	5	13	(4.4)	7	4	(3.5)	10	4	(2.3)	14
Rubiaceae	16	(4.1)	8	10	(3.4)	11	2	(1.8)	17	5	(2.9)	11
Heath forest > MDF												
Myrtaceae	27	(6.9)	2	16	(5.4)	4	11	(9.7)	1	14	(8.2)	4
Clusiaceae	18	(4.6)	6	8	(2.7)	13	6	(5.3)	4	15	(8.8)	2
Sapotaceae	6	(1.5)	22	6	(2.0)	15	5	(4.4)	6	6	(3.5)	7
MDF & heath forest similar												
Dipterocarpaceae	23	(5.9)	3	29	(9.7)	2	10	(8.8)	2	18	(10.5)	1
Lauraceae	23	(5.9)	4	15	(5.0)	6	6	(5.3)	4	6	(3.5)	7
Myristicaceae	18	(4.6)	6	13	(4.4)	7	5	(4.4)	6	7	(4.1)	6
Annonaceae	16	(4.1)	8	13	(4.4)	7	5	(4.4)	6	8	(4.7)	5
Ebenaceae	14	(3.6)	10	17	(5.7)	3	6	(3.5)	7	6	(3.5)	7
Anacardiaceae	11	(2.8)	11	16	(5.4)	4	6	(3.5)	7	6	(3.5)	7
Fabaceae	9	(2.3)	16	5	(1.7)	19	5	(4.4)	6	5	(2.9)	11

compared, so data for all trees (≥ 5 cm dbh) are presented. Note, however, that the percentage contribution of families did change (e.g. Araucariaceae and Dipterocarpaceae became more dominant at larger size classes). The Euphorbiaceae, Burseraceae and Tiliaceae were better represented in the MDF plots. The Myrtaceae were better represented in the heath plots, and the Araucariaceae were unique to them (Table 5). The Celastraceae were more dominant in the heath plots only in the larger size classes. The Dipterocarpaceae were the most important family in all plots except Badas, probably due to the dominance of *Agathis*. There were considerably more small-diameter dipterocarps at Sawat than at other plots, as indicated by their high contribution to stem abundance at that site. Between the heath plots, the Clusiaceae and Anacardiaceae contributed significantly more at Sawat than at Badas. Between the MDF plots there was slightly greater contribution by the Dipterocarpaceae and Sapotaceae at Ladan than Andulau, but otherwise family contributions to community structure were quite similar.

Table 5. Contribution of the more important families to basal area (ba) and stem abundance (n) in two MDF and two heath forest plots in Brunei Darussalam. All families by percentage contribution to basal area and stem abundance for trees ≥5 cm dbh. Figures in parentheses indicate the rank importance of the family for basal area or stem abundance in each plot. Family names with '-aceae' suffix removed.

	Mixed dipterocarp forest				Heath forest			
	Andulau		Ladan		Badas		Sawat	
	ba%	n%	ba%	n%	ba%	n%	ba%	n%
MDF > heath forest								
Euphorbi	4.2 (6)	11.7 (1)	5.2 (3)	16.7 (2)	0.6 (16)	2.5 (1)	1.9 (10)	6.4 (4)
Burser*	5.3 (4)	6.8 (3)	3.6 (6)	3.5 (9)	1.0 (11)	6.3 (5)	1.5 (12)	2.8 (10)
Tili	5.3 (3)	1.8 (16)	1.3 (13)	3.3 (11)	-	-	1.1 (15)	0.8 (21)
Heath forest > MDF								
Araucari	-	-	-	-	64.5 (1)	16.2 (2)	3.4 (6)	2.2 (14)
Myrt	4.0 (7)	5.1 (6)	3.7 (4)	2.3 (14)	7.2 (3)	28.4 (1)	7.8 (4)	8.2 (3)
MDF & heath forest no difference								
Dipterocarp	32.0 (1)	9.2 (2)	55.9 (1)	17.7 (1)	8.4 (2)	7.8 (3)	33.2 (1)	24.5 (1)
Anacardi	2.2 (13)	3.0 (12)	5.5 (2)	5.0 (3)	0.8 (14)	1.4 (15)	17.3 (2)	5.5 (6)
Fab	7.0 (2)	1.4 (21)	2.6 (8)	0.6 (27)	1.9 (6)	2.1 (10)	5.4 (5)	5.6 (5)
Clusi	4.7 (5)	4.0 (8)	0.8 (16)	2.0 (17)	1.5 (8)	2.9 (8)	7.9 (3)	9.6 (2)
Myristic	2.6 (10)	5.5 (4)	1.5 (10)	4.4 (5)	0.2 (20)	0.6 (20)	2.4 (9)	5.3 (7)
Sapot	1.2 (19)	1.7 (19)	3.7 (5)	5.0 (4)	1.8 (7)	2.1 (11)	2.5 (8)	2.5 (11)
Celastr	1.7 (16)	2.2 (14)	0.6 (20)	3.7 (7)	2.0 (5)	1.3 (16)	3.0 (7)	1.2 (18)
Sapind	0.3 (36)	1.8 (18)	0.3 (26)	0.8 (26)	2.1 (4)	6.6 (4)	0.2 (31)	0.9 (20)

* The Burseraceae contributed more to both basal area and abundance in the MDF plots at ≥10 cm dbh and ≥ 30 cm dbh.

Stand structure

Tree density and basal area

The distribution of subcanopy (10-30 cm dbh) and canopy (≥30 cm dbh) trees in all plots showed little pattern other than reduced numbers of canopy trees in low lying areas at Badas and Andulau (Figure 2). This was illustrated more clearly when the data were smoothed and contoured. High canopy tree basal areas were found on the ridges at Andulau, on the upslope at Ladan, and away from the depression at Badas. However, the highest basal area at Sawat occurred in the swampy depression (Figure 5). A similar but more striking pattern was shown by canopy tree densities (data not shown).

The low basal area in the depression at Badas was caused by the near absence of *Agathis borneensis* there. The very high basal area in the swamp at Sawat was attributable to numerous large individuals of *Gluta beccarii*. Brunig (1974) noted that very large basal areas in heath forest are often associated with adequate to abundant water supplies. Ashton (1964) observed that his valley plots at Andulau were characterised by a paucity of large trees, which was also seen in our plot.

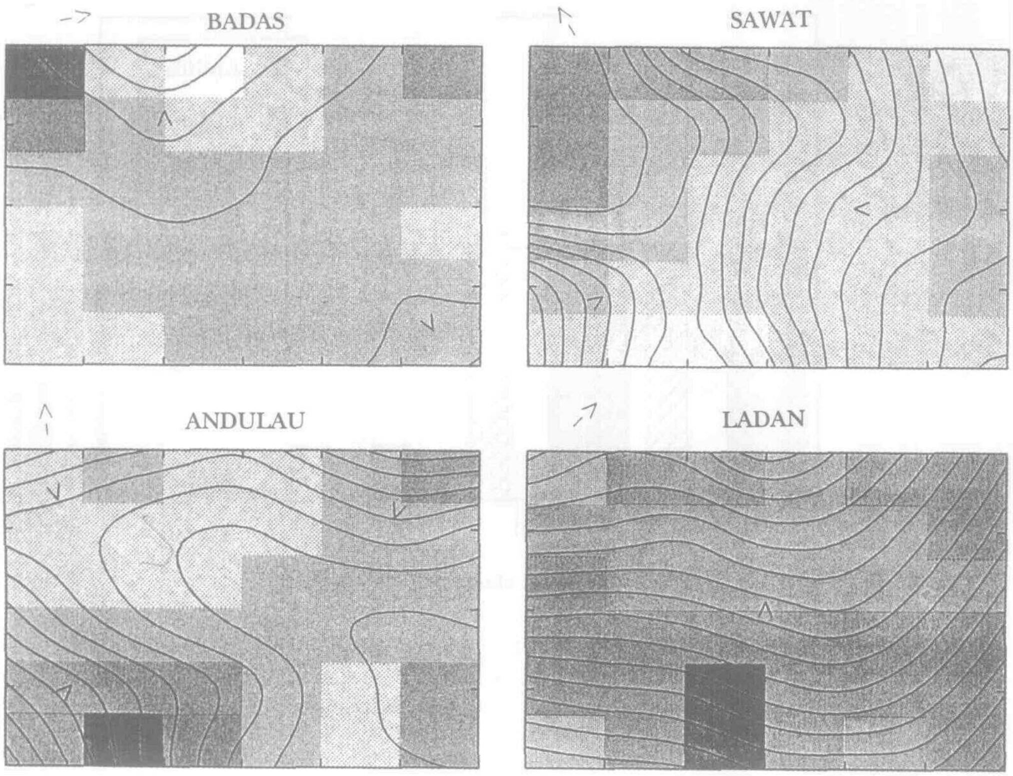

Figure 5. Basal areas (0, 1, 2, 3, 4 m^2 in order of increasing darkness) of trees ≥ 30 cm dbh in 20 × 20 m quadrats in two MDF and two heath forest plots in Brunei Darussalam. The data were smoothed by distance weighted least squares (Wilkinson 1990a).

Size class distributions

The size class distribution of trees ≥ 5 cm dbh in heath forest (Badas and Sawat) was not distinguishable from that in MDF (Figure 6). Brunig (1974) also noted that the diameter distribution of *Agathis borneensis* - dominated heath forest at Badas was not strikingly different from some of the distributions of dipterocarp forest. It was for trees 1-5 cm dbh in subsamples of the plots at Andulau, Ladan, Badas and Sawat, that Becker and Wong (1993) reported densities 40-100% greater in heath forest than in MDF.

Between plots within forest types there were some differences in tree diameter distributions. In the MDF plots, Ladan had a higher proportion of trees ≥ 30 cm dbh and a lower proportion of trees 5-10 cm dbh than Andulau, possibly suggesting that Andulau has been subject to more recent natural disturbance than Ladan. Between the heath plots the differences were small, but Sawat had a greater proportion of trees in the middle size classes (10-60 cm dbh) and fewer very large trees; this may be a consequence of the previous low intensity logging at this site, or the lower density of *Agathis borneensis*.

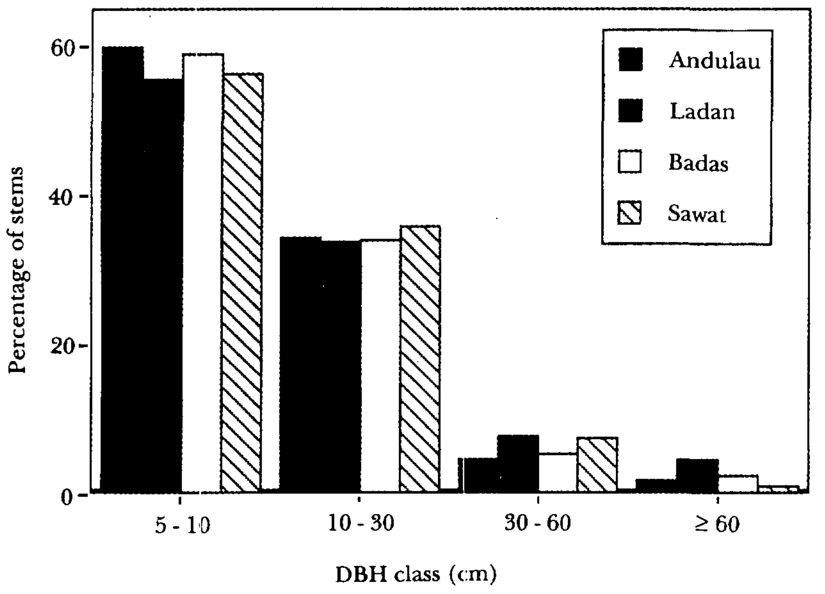

Figure 6. Diameter size class distribution of trees in two MDF (Andulau, Ladan) and two heath forest (Badas, Sawat) plots. Data are presented as proportions of total stems in each plot to account for among-plot differences in stand density.

Classification of vegetation types

Considerable effort was made to distinguish vegetation types within the Andulau and Badas plots, but several classification schemes revealed a remarkable floristic homogeneity (data not shown). The nonhierarchical, polythetic, divisive classification programmes COMPCLUS (Gauch 1979) and *k*-means (Wilkinson 1990b), and the hierarchical, divisive, polythetic programme TWINSPAN (Hill 1979) were employed. Analyses were made of 20 × 20 m quadrats and 10 × 10 m subquadrats for all species represented by at least 10 trees and for all species represented by trees ≥10 cm dbh (and occurring in at least two subquadrats at Andulau). Species occurrence was weighted by basal area, but additional analyses using data relativised within subquadrats or standardised within species were made to reduce the influence of dominant species. The clusters distinguished in these various analyses generally did not correspond with topographic variation, and in most cases there were numerous small clusters and little contiguity. This result was surprising because Newbery and Proctor (1984) were able to obtain a good classification of one hectare plots in heath and MDF using clusters of 10 × 10 m subquadrats formed at the first or second division by TWINSPAN. Moreover, association analysis of Ashton's (1964) original data for 0.4-ha plots at Andulau confirmed that stands on alluvium were mostly distinguishable from those on hillsides and ridges (Austin *et al.* 1972). This suggests that our plot was too small to detect the topographic component of floristic variation at Andulau.

Table 6. Species richness, SPP500® values, stem density, and basal area for trees ≥ 9.5, 9.7 or 10 cm dbh in primary lowland MDF and heath forest (≤ 400 m altitude) in Borneo. Soil nomenclature follows that used in the references. According to FAO-UNESCO - ISRIC (1988) soil nomenclature, red-yellow podzols would be acrisols (clay translocation and low base status = ultisol) or cambisols (moderately developed soil = inceptisol), gleys would be gleysol, and humus podsols or spodosols would be albic arenosols (≥ 0.5 m bleached horizon) or humic podzols (≤ 0.5 m bleached horizon).

Mixed dipterocarp forest

Site	Altitude (m)	Soil	Plot size (ha)	Species (ha^{-1})	SPP500	No. trees (ha^{-1})	Basal area (m^2 ha^{-1})	Reference
Sarawak								
G. Mulu	50	Humus podsol/gley	1.0	223		615	28	Proctor *et al.* (1983a)
G. Mulu	200	Red-yellow podsol	0.95	214+		778	57	Proctor *et al.* (1983a)
Lambir 2	114	Clay udult	0.6	212*	235	462	43	Phillips *et al.* (1994)
Lambir 3,4,5	114	Sandy humult	3 × 0.6	240*	195	739	53	Phillips *et al.* (1994)
Mersing	264	Basalt-derived clay luvisol	5 × 0.6	100*	134	438	44	Phillips *et al.* (1994)
Bako	30 - 75	Leached humult	5 × 0.6	195	165	656	35	Hall (1991)
Brunei								
Belalong	250	Shale-derived acrisol	1.0	231		550	41	Poulsen *et al.* (1996)
Ladan	70	Haplic acrisol	0.96	194+	194	500	42	This paper
Andulau	60	Sandy haplic acrisol & dystric fluvisols	0.96	256+	235	621	37	This paper
Sabah								
Sepilok-RP 17	30	Red-yellow podsolic	1.8	157*	138	666	42	Nicholson (1965)
Sepilok-RP 18	30	Ground water gley	1.0	117		435	38	Fox (1973)
DanumValley	60	Haplic acrisols & dystric cambisols	4.0	130*	138	470	27	Newberry *et al.* (1992)
Danum Valley	-	-	1.0	124		431	43	Kamaruddin (1986)
Kalimantan								
Berau	-	-	3 × 4			525	31	Sist (1995)
Lempake	40 - 80	Red-yellow podzolic	1.6	167*	177	445	34	Riswan (1987a)
Kutai	338	Red-yellow podzolic	6 × 0.8	-		-	43	Suselo & Riswan (1987)
Wanariset	50	Red-yellow podsolic	1.6	174*	170	541	30	Kartawinata *et al.* (1981)
Jaro	-	-	1.0	132*		399	40	Kartawinata *et al.* (1981)

continued

Table 6 (continued)

Heath forest

Site	Altitude (m)	Soil	Plot size (ha)	Species (ha^{-1})	SPP500	No. trees (ha^{-1})	Basal area (m^2 ha^{-1})	Reference
Sarawak								
Sabal	-	Podsol & spodosol	13.0	86		453	28	Weiscke (1995)
G. Mulu	170	Humus podsol	1.0	123		708	43	Proctor *et al.* (1983a)
Brunei								
Badas	20	Albic arenosol & gleyic podsols	0.96	77[+]	74	574	34	This paper
Sawat	20	Albic arenosol & humic podzol	0.96	121[+]	114	734	35	This paper
Sabah								
Sepilok-RP291	100	Podsol	5 x 0.04	65[#]		815-1285	20-50	Fox (1973)
Kalimantan								
G. Pasir 1	30	Podsol	0.5	24[#]		750	17	Riswan (1987b)
G. Pasir 2	30	Podsol	0.5	14[#]		554	6	Riswan (1987b)
Sebulu	150	Peaty, over white sandstone	-	-		549	11	Kartawinata (1980)

@ See note in Table 1. Missing values indicate unavailable data. Where species/tree number curves were provided (rarely the case), SPP500 values were directly interpolated; however, where only species/area curves were provided, SPP500 values were estimated by interpolating from the given tree density the area at which 500 trees would occur and hence from the species/area curve the species in 500 trees. This assumes that tree number is linearly related to area, which may not be the case. Because species/tree number curves are strongly non-linear, linear interpolations (e.g. species per 500 trees = species/stems x 500) of species per 500 trees will not be accurate and should be avoided.

[+]Observed number of species in plots slightly smaller than 1 ha.

*Estimates made from interpolation of species-area curves (see references cited).

[#]Total species richness for small plots.

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Discussion

Aspects of the stand structure and composition of the MDF and heath plots from this study are compared with other Bornean MDF and heath forests in Table 6. Although only a small number of forests from a restricted geographical range have been studied in detail, and a variety of methods have been used in the establishment of these plots, there is sufficient information to demonstrate that our plots are representative of their respective formations.

Among the MDFs studied, our two plots fall within the range of basal areas (27 - 57 $m^2 ha^{-1}$), stem densities (339 - 778 ha^{-1}), and close to the numbers for species richness (range: 130 - 240). The Andulau plot having 256 species (≥10 cm dbh) in 0.96 ha is extraordinarily species-rich, but is otherwise similar in community structure to the very species-rich MDF sites in northwest Borneo (Table 6, see also Hall 1991). Among the heath forests the Badas and Sawat plots appear reasonably typical, with stem density, basal area, and species richness all within the ranges reported for this formation (Table 6).

The data presented in Table 6 demonstrate the considerable structural variation among forests of both formations in Borneo. Species richness is almost always considerably higher in MDF. Basal area is typically less varied and higher in MDF though there is considerable overlap in the ranges. Stem densities (≥10 cm dbh) are not consistently different between the formations. From the limited data available, it would appear that the forests of the northwest of Borneo are considerably richer in species than those in eastern Borneo (especially Sabah). Interestingly, during the past century droughts have been more severe in eastern than in northwestern Borneo (Walsh 1995). They may provide an environmental filter which constrains species richness in the east, a point that will be taken up in a future paper. The low species richness on the fertile soils at Mersing (Hall 1991) is peculiar and remains unexplained. The depauperate heath plots at Gunong Pasir reported by Riswan (1987b) are clearly extreme, and as he suggests, may represent forests regenerating from recent disturbance.

Heath forest

Brunig (1974), and subsequently Newbery (1991) in a reanalysis of Brunig's data described a wide range of floristic and structural variation among the heath forests of Sarawak and Brunei. Variation among forests was broadly related to altitude which was also strongly correlated with soil type. In addition to high- and intermediate-elevation heath types, they identified a group of lowland stands occurring on medium-deep humus podzols (humic podzols to albic arenosols), frequently on coastal Pleistocene sands. Within this group there was a range of floristic and structural variation that appeared to be related to a drainage gradient, with *Agathis borneensis*-dominated stands at the well-drained end of the gradient and *Shorea albida*-dominated stands at the less well-drained end of the continuum.

Our plots belong to the group of coastal stands. Badas (an area also censused by Brunig) is typical of the *Agathis borneensis*-dominated, well-drained sites with stand structure and floristics similar to that described for Bukit Puan in Brunei (Forest Type 522.11: Brunig 1974, Ashton 1964). The Sawat plot also belongs to the coastal heath forest group, although *Agathis borneensis* is far less important. There is considerably greater topographic relief at Sawat than Badas (Figure 2), with the northern corner of the plot being quite swampy with some peat accumulation. In order to examine whether this was reflected in the floristics and/or structure of the plot, the proportions of species in the two heath plots were compared with species listed by Anderson (1972) as being common to the Peat Swamp Forests of Sarawak. The proportion of species common to Peat Swamps and to Badas or Sawat was high and not very different between the plots (Badas: 46 Peat Swamp species, 41% of the Badas species list; Sawat: 57 Peat Swamp species, 33% of the Sawat species list). However, considering abundance and basal area; typical Peat Swamp taxa accounted for 34% of stems and 49% of basal area at Sawat, and only 17% of stems and 14% of basal area at Badas.

It would appear that the increased habitat heterogeneity at Sawat does not contribute directly to increased species richness by contributing a greater proportion of species from the Peat Swamps than occurs at the less topographically variable plot, Badas. However, the topographic variation at Sawat with related areas of impeded drainage and probably shallower soils are a less favourable habitat for *Agathis borneensis* (Wood 1965, and Brunig 1974, comment on the importance of deep well-drained white-sand podzols for *Agathis borneensis*).Therefore, its lack of dominance at Sawat has led to greater evenness in species composition and consequently higher species richness.

Mixed dipterocarp forest

MDF accounts for the greatest proportion of the lowland forests of Borneo. It is structurally and compositionally greatly variable throughout Borneo (Table 6, see references therein; Hall 1991, Ashton & Hall 1992). The extreme species richness, the typical lack of dominant species, and the localised distribution of many main canopy species in MDFs have combined to make the delimitation of MDF sub-types difficult on a Bornean scale (Ashton 1964, Brunig 1969, Whitmore 1984).

For MDFs in Sarawak and Brunei, Ashton (1964) and Hall (1991) demonstrated floristic and structural variation among forests growing on a wide range of soils and parent materials. At least among these sites in Sarawak and Brunei, broad-scale floristic variation appears to be related to a gradient in both soil clay content and leaching (indicating variation in base saturation) which in turn influence soil nutrient availability (Baillie *et al.* 1987, Hall 1991). Topography, drainage, and geography are also evidently important in contributing to this pattern (Austin *et al.* 1972, Proctor *et al.* 1983a). Grip *et al.* (1994) have shown that shale bedrock contains substantially higher amounts of K, Na, Mg and S than sandstone, and produces plant nutrients by weathering at a faster rate. Thus, the following description is a simplification of a complex gradient. At one extreme of this gradient are the MDFs growing on humic acrisols over sandstone, with the most strongly leached of these (e.g. Bako, Hall 1991) having considerable floristic similarity to heath forests. Also on sandstone, is a wide range of forests growing on sandy haplic acrisols with low to moderate clay content and a tendency to humus accumulation above the A-horizon (e.g. Andulau, Ashton 1964; Lambir plots 3-5, Hall 1991). Austin *et al.* (1972) demonstrated that local variation in the composition of MDF on sandy haplic acrisols at Andulau was related to drainage and the degree of soil leaching. Further along this gradient are the forests on clay-rich haplic acrisols developed over shale or interbedded sandstone and shale, with higher clay and nutrient contents (e.g. Belalong, Ashton 1964, Poulsen *et al.* 1996; Lambir plot 2, Hall 1991, Phillips *et al.* 1994). Austin *et al.* (1972) demonstrated that local variation in forests growing on clay-rich haplic acrisols was related to both topography and altitude. The forests on basalt-derived soils (e.g. Mersing, Hall 1991) are at the nutrient- and clay-rich end of the gradient, with particularly high soil phosphorus content and base saturation (Hall 1991). These forests share floristic similarity with the forests on clay-rich haplic acrisols, but also appear to have a number of unique floristic characteristics.

To understand our Andulau and Ladan plots in the context of this gradient, we compared the species composition of Dipterocarpaceae between each of the forests studied by Ashton (1964) and Hall (1991) with the plots in our study. This comparison was restricted to Dipterocarpaceae because of the overall importance of the family in these forests, and the high likelihood of consistent species identification among the plots. Although there was variation in the size of the plots, it was thought probable that the samples were representative of the respective sites. The floristic similarity between plots generally agreed with the continuum described above, with plots from similar soil types appearing floristically more similar than plots from more different soil types (Table 7). The heath plots at Badas and Sawat were most similar to each other (J_a = 0.60), but shared considerable floristic overlap with the humic acrisol plots at Bako (J_a = 0.30-0.44), and the sandy haplic acrisols at Andulau (J_a = 0.43-0.46). The humic acrisol plots at Bako were most similar to the heath plots at Badas and Sawat. Dipterocarp similarity was high among the sandy haplic acrisol plots themselves (J_a = 0.54 - 0.82), but they also shared some floristic overlap with both the clay-rich acrisols at Ladan (J_a = 0.20 - 0.42) and Belalong (J_a = 0.16 - 0.34), and the humic acrisols at Bako (J_a = 0.16-0.18). The clay-rich haplic acrisol plots shared minimal dipterocarp similarity with Bako and the heath plots (J_a = 0.00 - 0.17), and higher similarity with the other clay-rich plots (J_a = 0.11- 0.38). However, especially in the case of Ladan, they also shared some overlap with the sandy haplic acrisol plots. The clay-rich basalt luvisol at Mersing showed generally the least similarity to the other plots, but overlap was greatest with the clay-rich haplic acrisol plots at Belalong (J_a = 0.42).

Of the two MDF plots in our study, Andulau was similar to the plots on sandy haplic acrisol soils at Lambir (L-345, J_a = 0.61), and was representative (J_a = 0.82) of the Andulau plots of Ashton (1964). Ladan shared high dipterocarp similarity with both the sandy and clay-rich haplic acrisols (And-64 J_a = 0.42, Belalong J_a = 0.36). The soils at Ladan have relatively higher clay content than Andulau, being derived from interbedded shale and sandstone, whereas the soils of Belalong and Lambir (L-2) are shale-derived. Ashton (1964) described the Ladan-type soils as clay latosols with an important indicator dipterocarp being *Dipterocarpus verrucosus*, which was present at Ladan. Floristically, the plot appears intermediate between the Andulau and Belalong plots and this may correspond to soil features; however, other factors such as limitations in sampling need to be assessed.

Table 7. Similarity indices (adjusted Jaccard's coefficient@) of Dipterocarpaceae species composition among MDF and heath forest plots in Sarawak and Brunei. Figures underlined for each column show the comparisons with relatively high floristic similarity (≥ 0.3) between plots.

Soil*		Badas+	Sawat	Bako	And-96	And-64	L-345	Ladan	L-2	Belalong	Mersing
AA-	Badas	-	0.60	0.44	0.07	0.46	0.08	0.00	0.00	0.00	0.00
P/AA-	Sawat	0.60	-	0.30	0.03	0.43	0.12	0.04	0.04	0.09	0.00
HA-	Bako	0.44	0.30	-	0.18	0.18	0.16	0.04	0.16	0.17	0.05
SHA-	And-96	0.07	0.03	0.18	-	0.82	0.61	0.20	0.07	0.24	0.00
SHA-	And-64	0.46	0.43	0.18	0.82	-	0.54	0.42	0.16	0.16	0.05
SHA-	L-345	0.08	0.12	0.16	0.61	0.54	-	0.25	0.22	0.34	0.10
CHA-	Ladan	0.00	0.04	0.04	0.20	0.42	0.25	-	0.11	0.36	0.04
CHA-	L-2	0.00	0.04	0.16	0.07	0.16	0.22	0.11	-	0.38	0.08
CHA-	Belalong	0.00	0.09	0.17	0.24	0.16	0.34	0.36	0.38	-	0.42
BL-	Mersing	0.00	0.00	0.05	0.00	0.05	0.10	0.04	0.08	0.42	-

@ Due to differences in sample sizes between comparisons Jaccard's coefficient of similarity was adjusted to the proportion of maximum possible similarity for each comparison (i.e. adjusted $J_a = J/J_{max}$ where $J_{max} = J$ if all species in sample 1 were also found in sample 2).

* Soil categorisation: AA, albic arenosol; P, humic podzol; HA, humic acrisol; SHA, sandy haplic acrisol; CHA, clay-rich haplic acrisol; BL, clay-rich basalt-derived luvisol.

+ Data from the following sources: Badas, Sawat, And-96 (Andulau) and Ladan from the present study; And-64 (Andulau) and Belalong from Ashton (1964); and Bako, L-345 and L-2 (Lambir plots 3,4,5 & 2) and Mersing from Hall (1991).

In conclusion, there is considerable floristic and structural variation within and among the MDF and heath forests of Borneo. Following Proctor *et al.* (1983a) and Newbery *et al.* (1992), it seems unlikely that single factors (e.g. soils, topography, drainage) function independently in determining floristic variation or are together independent of vegetation interactions. It is necessary to continue experimental studies (Anderson *et al.* 1983, Proctor *et al.* 1983b) to elucidate the relative importance of some of these factors in influencing forest structure and composition. The forests selected for this study seem representative of their formations and appropriate for comparative ecophysiological studies.

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