

STAND STRUCTURE AND FLORISTIC COMPOSITION OF A PRIMARY LOWLAND DIPTEROCARP FOREST IN EAST KALIMANTAN

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SIST, P. & SARIDAN, A. 1999. Stand structure and floristic composition of a primary lowland dipterocarp forest in East Kalimantan. This paper presents the structure and species composition of the primary lowland dipterocarp forest in Berau, East Kalimantan, Indonesia. This study was based on three undisturbed forest plots, 4 ha each, totalling 12 ha, where 93% of the trees (dbh \geq 10 cm) were identified at the taxa level. The density, basal area and standing volume were on average and respectively 521 trees ha⁻¹, 31 m² ha⁻¹ and 383 m³ ha⁻¹. The dipterocarps represented about 25% of the tree population, 50% of the basal area and 60% of the standing volume. In primary forest 538 different taxa were recognised representing a mean of 182 tree species per ha. The families Dipterocarpaceae and Euphorbiaceae were the main important taxa in both density and number of species (61 species each). The structure of the forest of Berau is very similar to that of Sabah or other parts of Northern Borneo. However, the main characteristic of this forest is its remarkable richness in dipterocarps, in comparison with the northern parts of Borneo, which exhibits in mean 29 species ha⁻¹ and 61 species for the 12 ha surveyed. The forests of Sabah are mainly dominated by light-demanding dipterocarp species such as *Parashorea* spp. and *Dryobalanops* spp. This could result from important canopy disturbances caused by climatic events like long period of drought or cyclone. The high species richness of the Berau forest may be linked to a longer stability and a relative constancy of the climate in the region. The hypothesis of a possible impact of drought events on the forest dynamics and consequently on species distribution and richness in Borneo is discussed. However, it is stressed that the lack of data for Kalimantan is undoubtedly an handicap for the analysis of phytogeographical variations within the region. In the study area, the first record for Indonesia of the two dipterocarps species *Shorea leptoderma* Meijer and *Shorea symingtonii* Wood demonstrates that our knowledge of the flora of Kalimantan is still to be improved.

Key words: East Kalimantan - Borneo - primary lowland dipterocarp forest -structure - species richness

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SIST, P. & SARIDAN, A. 1999. Struktur dirian dan komposisi flora hutan dipterokarpa tanah pamah primer di Berau, Kalimantan Timur. Artikel ini membentangkan mengenai struktur dan komposisi spesies hutan dipterokarpa tanah pamah primer di Berau, Kalimantan Timur, Indonesia. Kajian ini didasarkan kepada tiga petak hutan tidak rosak, setiap satu seluas 4 ha, berjumlah 12 ha iaitu 93% daripada pokok tersebut (dbh > 10 cm) dikenal pasti pada peringkat taksa. Kepadatan, luas pangkal dan isipadu dirian ialah pada kadar purata dan masing-masing ialah 521 pokok sehektar, 31 pokok sehektar, dan 383 m³ ha⁻¹. Dipterokarpa mewakili kira-kira 25% daripada populasi pokok, 50% daripada luas kawasan dan 60% daripada isipadu dirian. Di dalam hutan primer, 538 taksa yang berbeza dikenali mewakili sebanyak 182 spesies pokok sehektar. Famili Dipterocarpaceae dan Euphorbiaceae merupakan taksa yang penting dalam kedua-dua kepadatan dan bilangan spesies (61 spesies setiap satu). Struktur hutan di Berau sama dengan struktur hutan di Sabah atau bahagian-bahagian lain di Borneo Utara. Bagaimanapun, ciri utama hutan ini ialah kekayaan dipterokarpnya, berbanding dengan bahagian utara Borneo, yang mempamerkan secara purata 29 spesies sehektar dan 61 spesies bagi 12 hektar yang disurvei. Hutan di Sabah kebanyakannya didominasi oleh spesies dipterokarpa yang memerlukan banyak cahaya seperti *Parashorea* spp. dan *Dryobalanops* spp. Ini mungkin terjadi akibat gangguan sudur yang penting akibat gangguan cuaca seperti tempoh kemarau atau taufan yang lama. Kekayaan spesies di hutan Berau mungkin ada kaitannya dengan kestabilannya dan ketetapan cuaca secara relatif di kawasan tersebut. Hipotesis mengenai kemungkinan kesan kemarau terhadap dinamik hutan dan seterusnya terhadap taburan dan kekayaan spesies di Borneo juga turut dibincangkan. Bagaimanapun, ditekankan bahawa kekurangan data bagi Kalimantan tidak syak lagi merupakan satu hambatan untuk menganalisis kepelbagaian fitogeografi di kawasan tersebut. Di kawasan yang dikaji, catatan pertama bagi Indonesia untuk dua spesies dipterokarpa iaitu *Shorea leptoderma* dan *Shorea symingtonii* menunjukkan bahawa pengetahuan kita mengenai flora di Kalimantan masih perlu ditingkatkan.

Introduction

Borneo is widely acknowledged as one of the most important centres of plant diversity in the world as well as the centre of distribution and species diversity for a large number of families and genera (Van Steenis 1950, Whitmore 1984, Soepadmo 1995). Within the Malesian archipelago, the greatest number of dipterocarp species has been recorded in Borneo which includes 267 species with 59% of endemism (Ashton 1982). In comparison, species number and endemism are respectively in Malaysia 156 and 19%, in Sumatra 96 and 12%, in the Philippines 45 and 47%. Although New Guinea shows the highest endemism for dipterocarps (73%), and generally speaking for the other taxa, it is also the poorest island with only 15 species (Ashton 1982). In the western block of the Malesian archipelago, the lowland evergreen tropical rain forest is called lowland dipterocarp forest because of the dominance in the canopy and the emergent stratum of the family of the Dipterocarpaceae. This forest shows the greatest number of species of any rain forest ecosystem in Malesia (Whitmore 1984, Philips *et al.* 1994). The dipterocarp forests of Borneo are also one of the most productive in the tropics since harvesting rates range from 80 to 100 m³ ha⁻¹ whereas in other parts of the tropics they do not exceed 30 to 50 m³ ha⁻¹ (Schmidt 1991, Bertault & Sist 1997, Sist *et al.* 1998).

The ecology of dipterocarp forests has been widely studied particularly in Peninsular Malaysia and in the northern parts of Borneo (most important references : Symington 1943, Wyatt-Smith 1966, Poore 1968, Kochummen *et al.* 1991, Appanah & Weinland 1993 for Peninsular Malaysia; Burgess 1961, Ashton 1964, Bruenig 1973, Proctor *et al.* 1983, Baillie *et al.* 1987, Ashton & Hall 1992, Newberry *et al.* 1992, Davies & Becker 1996 for Sabah, Sarawak and Brunei). Several studies have demonstrated that floristic variation within tropical rain forest is linked to the complex interaction of both physical (climate variation, cyclone, edaphic conditions, topography) and biological factors (forest dynamics, species growth requirements during development) (Ashton 1969, 1989, Raich & Khoon 1980, Bruenig 1970, Gentry 1989, Hartshorn 1989, Philips & Gentry 1994). For the Indonesian part of the Island (Kalimantan), studies on the ecology of mixed dipterocarp forest are relatively new (Kartawinata *et al.* 1981, Riswan 1987, Suselo & Riswan 1987, Soedjito & Kartawinata 1995). Although a species check list of all the families with at least one timber size species has been published for Indonesia (Whitmore *et al.* 1990), the tree flora of Indonesia is still at a preliminary stage.

This study was carried out in the framework of STREK (Silvicultural Techniques for the Regeneration of Logged-over Forests in East Kalimantan) project which aimed to maintain sustained productivity of the forests of East Kalimantan by the experimentation of logging improvement techniques (Reduced-Impact Logging or RIL) in primary forest and silvicultural treatments in logged-over forests (Bertault & Sist 1995, 1997, Sist *et al.* 1998). Because sound forest management cannot possibly be applied without an understanding of the basic ecology of the forest, research on forest structure and species composition was an important component of the project. This paper presents the main results of the project regarding the structure and species composition of three 4-ha plots in a primary undisturbed lowland dipterocarp forest in East Kalimantan.

Materials and methods

Study area

The study area was located in East Kalimantan (Indonesia) in the district of Berau (2°N, 117° 15'E), in a 500 000 ha of forest concession (Figure 1). The concessionaire, PT INHUTANI I, a state-owned company, has been harvesting timber in this area for the past fifteen years. The climate is equatorial with a mean annual rainfall of 1870 mm (SD = 240 mm, records for Tanjung Redeb, 1984-1994) and a mean annual temperature of about 25 °C. August and September are usually the driest months while January is the wettest one (Figure 2). The bedrock is primary alluvial deposits (mudstones, siltstones, sandstone and gravel) dating from Miocene and Pliocene. The topography is gently undulating with elevations above sea-level below 500 m.

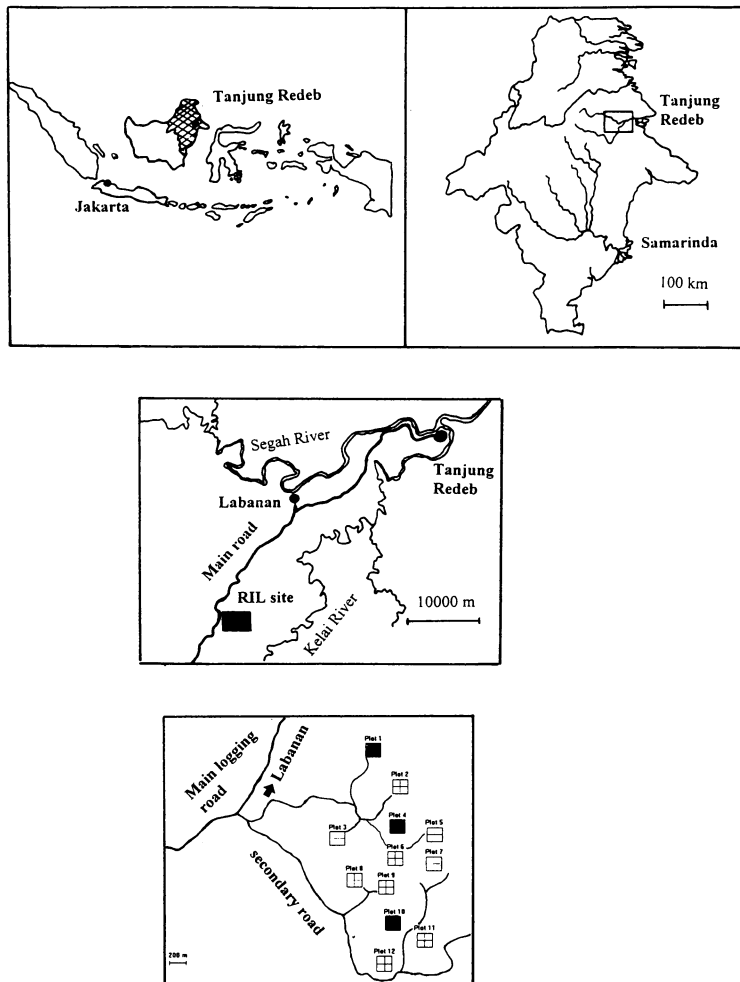


Figure 1. Map of Indonesia, East Kalimantan and location of the experimental plot network in the study area

Methods

A 5% inventory within the 1000-ha zone scheduled for logging provided the data base for sample plot selection. Twelve 4-ha plots (200 × 200 m), each divided into four 1-ha subplots, were set up in 1989. From November 1991 to March 1992, logging operations were carried out in nine plots following conventional and RIL techniques (Bertault & Sist 1995, 1997, Sist *et al.* in press) whereas three plots (1, 4, 10) remained undisturbed as control plots. In each control plot, slopes were measured every 10 m, along 20 tracks, 200 m long with a south–north direction. These data were then processed with Surfer software for the map drawing and used

as base maps for soil survey. In each control plot 25 augerings, displayed every 50 m, up to 110 cm depth, were collected and the following soil characteristics described: geomorphology, slope classification, soil drainage, soil type, parent material and texture. On the basis of information provided by the augerings, representative sites were selected for the detailed description of soil profiles in pits with a 150 cm depth.

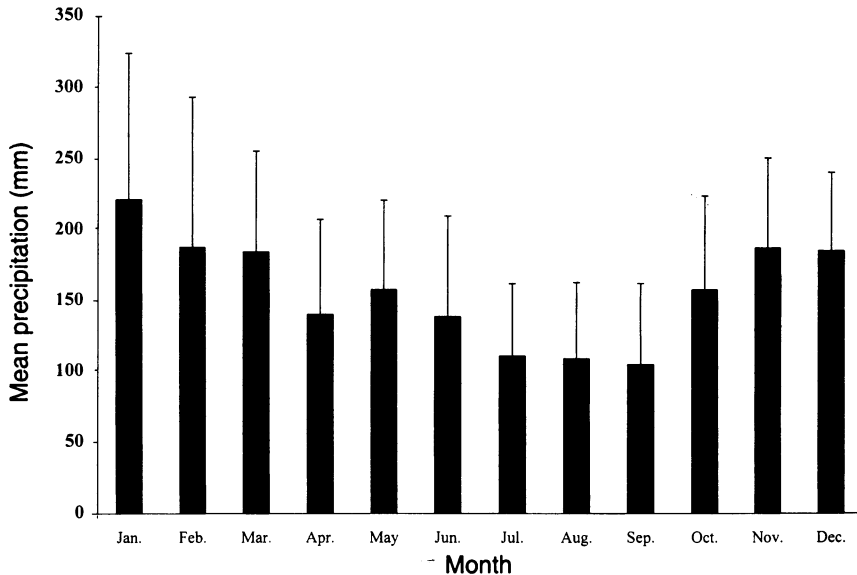


Figure 2. Mean annual rainfall (+SD) in Tanjung Redeb for the period 1984–1994

Before logging commenced, all trees with dbh ≥ 10 cm were measured (girth at 1.30 m or 20 cm above buttresses), numbered and marked. Plant collections were made and herbarium samples identified in Bogor (Herbarium Bogoriense). Because of time constraint in the logging operation schedule, tree identification at the species level could not be achieved before logging. However, this was completed in the three undisturbed plots in 1994.

Jaccard's coefficient was used to compare the floristic similarity of the three control plots. This coefficient was: $J = c / (a + b - c)$ where c is the number of common species between a pair of plots, a and b the total number of species in each plot (Dajoz 1982).

Results

Soil characteristics

The analysis of the 75 augerings in the three undisturbed forest plots gave the following records (SSS classification, 1987): Ultisols (93%), Entisols (7%). Ultisols comprised Paleudults and Hapludults which are deep with an illuvial B horizon of low base saturation ($BS < 35\%$). These two types of soil differ mainly from each other in the deeper illuvial horizon of Paleudults. Paleudults and Hapludults were recorded in roughly similar proportions, 41% and 52% respectively. Paleudults and Hapludults are classically divided in Typic (well to moderately drained) or Aquic (bad or impeded drainage). Most of the Paleudults (74%) were well drained (typic) whereas Hapludults showed in general a bad drainage pattern (79%). Entisols were described as Lithic Tropeorthents mainly characterised by their shallow development (less than 40 cm deep), a good drainage pattern and a loamy to sandy loamy texture.

Plots 1 and 4 were very similar in both soil type, drainage and topography (Table 1). They were mainly located on a plateau with Typic Paleudult and Typic Hapludult suggesting therefore good drainage conditions. In contrast, plot 10 showed a much steeper relief and lay on poor drained Ultisols (Table 1).

Table 1. Soil characteristics in plots 1, 4 and 10 (results of the 75 augerings collected in the three plots, 25 augerings in each)

	Ultisols				Entisols	Drainage	
	TP	AP	TH	AH	LT	1-2	3-4
Plot 1	14	5	4	2	0	7	18
Plot 4	8	2	4	6	5	16	9
Plot 10	1	1	0	23	0	23	2
Total	23	8	8	31	5	46	29
%	30	11	11	41	7	61	38

TP: Typic Paleudults, AP : Aquic Paleudults, TH, AH: Typic and Aquic Hapludults, LT: Lithic Tropeorthents. Drainage: 1-2: Poorly to imperfectly drained, 3-4: Moderately well to well drained.

Forest structure and tree family

In primary forest, tree density, basal area and standing volume were on average and respectively, 521 trees ha^{-1} , 31 $\text{m}^2 \text{ha}^{-1}$ and 383 $\text{m}^3 \text{ha}^{-1}$ (Table 2). The family of Dipterocarpaceae was the dominant taxon gathering about 25% of the total tree density (126 stems ha^{-1} in mean), 50% of the total basal area (15 $\text{m}^2 \text{ha}^{-1}$) and 61% of the stand volume (234.5 $\text{m}^3 \text{ha}^{-1}$, Table 2).

Table 2. Mean density (MD), mean basal area (MBA), and mean stand volume (MSV) of all trees and dipterocarps only according to the dbh classes in the three control plots (12 ha) of primary forest

	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	>100 cm	Total
All trees											
Mean density (No. ha ⁻¹)	329.1	93.6	45.3	20.9	12.0	8.6	4.2	3.1	1.5	3.1	521.3
SD	41.8	11.8	7.3	5.1	4.2	3.5	2.6	1.7	1.3	1.9	53.1
Mean basal area (m ² ha ⁻¹)	5.0	4.4	4.3	3.3	2.8	2.8	1.8	1.7	1.1	4.0	30.6
SD	0.6	0.6	0.7	0.8	1.0	1.2	1.1	0.9	1.0	2.2	3.1
								> 90 cm			Total
Mean standing volume	37.8	43.7	49.4	40.8	36.5	42.8	28.2	26.2	77.4		382.9
SD	4.4	6.3	10.1	10.2	16.8	17.7	17.5	11.7	39.7		60.7
Dipterocarps											
Mean density	60.3	21.9	13.4	7.4	7.1	6.2	2.6	2.6	1.4	3.0	125.8
SD	12.4	5.3	6.9	3.9	3.8	2.7	2.6	1.6	1.4	1.9	25.1
Mean basal area	0.9	1.0	1.3	1.2	1.6	2.0	1.1	1.4	1.0	3.2	14.9
SD	0.21	0.2	0.6	0.6	0.9	0.9	1.1	0.9	1.0	2.5	3.3
								> 90 cm			Total
Mean standing volume	10.1	11.8	16.2	18.4	27.4	32.8	23.9	28.0	74.0		234.4
SD	2.3	3.6	8.2	9.9	14.0	14.0	19.6	29.9	44.4		53.3

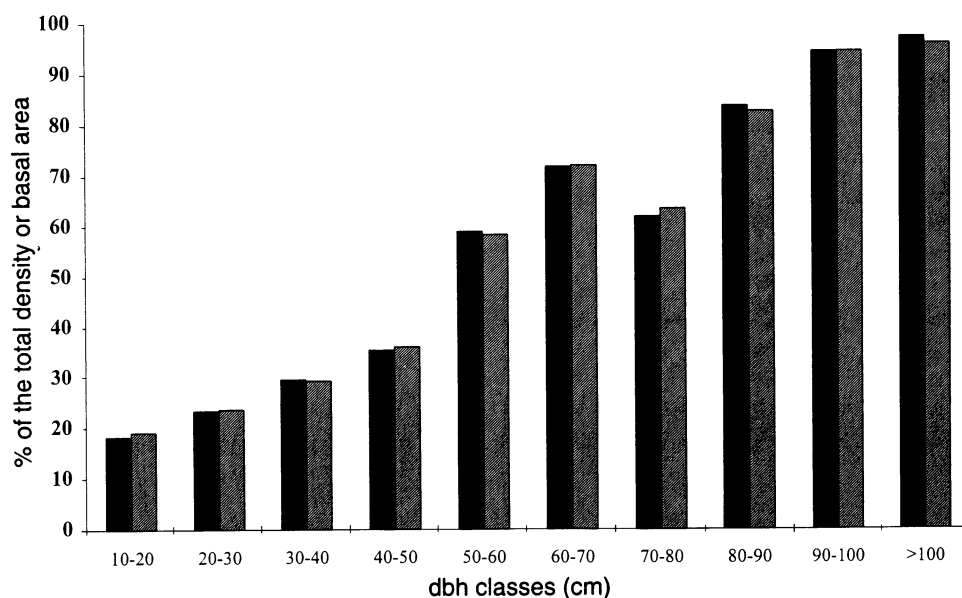


Figure 3. Proportions of dipterocarps in basal area and density in each diameter class (solid bars: % of the total basal area ; hatched bars: % of the total tree density, area surveyed: 12 ha, 3 undisturbed forest plots)

Table 3. Cumulated density of each family in the three control plots according to the dbh classes

	DBH classes (cm)							Total	N sp	% dens.	% BA
	10-19	20-29	30-39	40-49	50-59	60-69	>70				
Dipterocarpaceae	727	263	160	86	89	72	113	1510	61	24.14	48.73
Euphorbiaceae	551	164	83	38	7	1	1	845	61	13.51	9.02
Sapotaceae	312	58	16	4	4	3	1	398	20	6.36	3.14
Myristicaceae	287	58	7	3	0	0	0	355	19	5.68	2.22
Burseraceae	235	46	11	11	3	1	2	309	21	4.94	2.80
Myrtaceae	140	77	32	11	3	2	2	267	22	4.27	3.50
Ebenaceae	165	55	21	5	1	1	0	248	17	3.96	2.28
Leguminosae	131	33	31	15	12	4	8	234	26	3.74	4.60
Anacardiaceae	142	36	21	11	4	0	2	216	26	3.45	2.56
Lauraceae	104	33	26	18	4	3	1	189	23	3.02	2.98
Annonaceae	144	19	4	1	0	0	0	168	18	2.69	0.98
Rubiaceae	121	31	9	1	0	1	0	163	20	2.61	1.26
Guttiferae	86	27	9	5	2	0	0	129	20	2.06	1.25
Unknown	94	29	12	5	6	3	4	153	5	2.45	2.16
Moraceae	68	18	15	5	1	1	0	108	12	1.73	1.26
Sterculiaceae	44	14	14	9	2	3	1	87	7	1.39	1.63
Polygalaceae	59	8	4	3	0	0	1	75	14	1.20	0.68
Fagaceae	32	17	14	3	1	0	0	67	20	1.07	0.92
Meliaceae	42	11	6	1	3	0	1	64	16	1.02	0.81
Verbenaceae	37	17	8	0	0	0	2	64	6	1.02	0.92
Sapindaceae	28	15	4	2	0	0	0	49	11	0.78	0.47
Melastomataceae	41	2	1	0	0	0	0	44	8	0.70	0.20
Lecythidaceae	31	13	0	0	0	0	0	44	4	0.70	0.31
Elaeocarpaceae	31	6	5	0	0	0	0	42	12	0.67	0.32
Thymelaeaceae	27	5	4	0	1	0	0	37	9	0.59	0.41
Chrysobalanaceae	24	8	2	3	0	0	0	37	9	0.59	0.36
Tiliaceae	21	6	3	0	5	1	0	36	4	0.58	0.67
Flacourtiaceae	23	3	2	0	0	0	1	29	6	0.46	0.30
Bombacaceae	18	8	0	3	0	0	0	29	5	0.46	0.29
Dilleniaceae	25	2	1	0	0	0	0	28	2	0.45	0.18
Icacinaeae	21	7	0	0	0	0	0	28	4	0.45	0.16
Ulmaceae	20	4	0	0	0	0	0	24	3	0.38	0.24
Celastraceae	16	3	4	1	0	0	0	24	6	0.38	0.12
Loganiaceae	18	4	0	0	0	0	0	22	2	0.35	0.57
Oleaceae	14	5	2	0	1	0	0	22	2	0.35	0.12
Apocynaceae	8	5	3	3	0	3	0	22	2	0.35	0.21
Myrsinaceae	18	1	0	0	0	0	0	19	1	0.30	0.10
Rhamnaceae	15	2	0	0	0	0	0	17	3	0.27	0.07
Theaceae	8	5	0	0	0	1	0	14	4	0.22	0.22
Ochnaceae	6	6	0	0	0	0	0	12	1	0.19	0.11
Symplocaceae	6	2	1	0	0	0	0	9	1	0.14	0.08
Magnoliaceae	6	0	0	0	0	0	0	6	1	0.10	0.02
Araucariaceae	2	0	0	0	0	2	1	5	1	0.08	0.61
Simaroubaceae	2	1	1	0	0	0	0	4	1	0.06	0.07
Olacaceae	0	0	2	0	0	0	0	2	1	0.03	0.05
Tetrameristaceae	0	0	1	0	0	0	0	1	1	0.02	0.02
Total	3950	1127	539	247	149	102	141	6255	538	100	100

Nsp: Cumulated total number of species in the family, % dens.: % of the family in the tree population, % BA : % of the family's basal area of the total basal area.

The distribution of the basal area according to diameter classes clearly indicated that dipterocarps mainly dominated the upper dbh classes and were therefore canopy and emergent trees (Table 3, Figure 3). In the three undisturbed forest plots, 70% of the trees with dbh (> 50 cm) belonged to the Dipterocarpaceae family and to the following genera: *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Parashorea* and *Shorea*. The other two genera of dipterocarps, *Vatica* and *Hopea*,

rarely exceeded 50 cm in diameter and were found mainly in the understorey and subcanopy layers. The Euphorbiaceae was the second most abundant family comprising 13.5% of the total tree density and 9% of the basal area (Table 3). This taxon comprised mainly understorey and medium-sized trees which did not generally exceed 50 cm in diameter (Table 3). The few species reaching a dbh greater than 50 cm that have been recorded in the control plots were *Chaetocarpus castanocarpus*, *Drypetes kikir* and *Elatiospermum tapos*. The number of taxa recorded in the second richest families, namely Anacardiaceae and Leguminosae, dropped to only 26.

Fourteen families (Dipterocarpaceae, Euphorbiaceae, Sapotaceae, Myristicaceae, Burseraceae, Myrtaceae, Ebenaceae, Leguminosae, Anacardiaceae, Lauraceae, Annonaceae, Rubiaceae, Guttiferae, Moraceae) comprised 82% of the total tree density and 68% (i.e. 366) of the taxa recorded in the three control plots (Table 3).

The distribution of the families according to the dbh classes allowed distinguishing four main groups of trees: 1) canopy and emergent trees, 2) medium-sized trees (subcanopy to canopy trees), 3) small trees of the understorey, 4) pioneer species. The first group is mainly dominated by dipterocarps with, however, some Leguminosae such as *Koompassia excelsa*, *K. malaccensis* and *Sindora* spp. Some Sterculiaceae (*Heritiera simplicifolia*, *Scaphium macropodum*) and Tiliaceae like *Pentace adnophora* can be also found in the canopy layer. The second includes medium-sized trees which did not generally exceed 70 cm in diameter. In primary forest, this group comprised mainly the following families: Anacardiaceae, Burseraceae, Ebenaceae and Sapotaceae. The commonest species in this group were *Gluta renghas* and *Buchanania* spp. (Anacardiaceae), *Canarium* sp. *Dacryodes costata* and *D. rostrata* (Burseraceae), *Diospyros endertii* and *D. bornensis* (Ebenaceae), *Madhuca malaccensis*, *Madhuca* sp. 2 and *Palaquium ericalyx* (Sapotaceae). Group 3 comprised small trees (dbh < 50 cm) which mainly belong to the following families: Annonaceae (*Polyalthia rumphii*, *P. sumatrana*, *Goniothalamus macrophyllus*), Euphorbiaceae (*Aporosa* spp. *Baccaurea sumatrana*), Guttiferae (*Mesua borneensis*), Moraceae (*Artocarpus anisophyllus*, *A. lanceifolius*), Myristicaceae (*Knema laurina*, *K. furfuracea*, *Gymnacranthera forbesii*, *Myristica iners*) and Rubiaceae (*Nauclea* sp.). The fourth group includes fast-growing pioneer species colonising opened areas like big gaps. These trees are mainly *Macaranga gigantea*, *M. hypoleuca*, *M. pruinosa*, *M. triloba* (Euphorbiaceae), *Anthocephalus chinensis* (Rubiaceae), *Duabanga mollucana* (Sonneratiaceae) and *Octomeles sumatrana* (Datiscaceae).

Species identification rate

The three control plots comprised 6255 trees with dbh ≥ 10 cm. Among these 6255 trees, 6102 (97.5%) were identified at the family level whereas 153 (2.5%) remained as unknown taxa or unidentified trees. All the trees could not be collected and identification was achieved for 5764 trees (92.3% of the tree population) sorted into 538 different taxa comprising 45 families and 128 genera. Among these taxa, 280 were identified to species level ($n = 4320$ trees or 69.2% of the total tree

population) while 185 ($n=1122$ or 17.9 % of the trees) and 68 ($n=293$ or 4.7%) were identified to the genus and family levels respectively. Five taxa ($n=29$ or 0.5 %) remained as unknown families.

Species richness

The tree ($\text{dbh} \geq 10$ cm) taxa were 329 in plot 1, 358 in plot 4 and 322 in plot 10 with on average, 182 species per hectare ($\text{SD} = 16.6$, $n = 12$, minimum = 160 species in plot 10 square 3, maximum = 201 species in plot 1 square 3). A 4-ha sample plot was not representative of the species richness of the primary forest since it comprised on average 63% of the total taxa identified in the overall 12-ha sampled area. The species–area curve confirms this result and shows that, in each plot the asymptote was not reached for a 4-ha inventory (Figure 4).

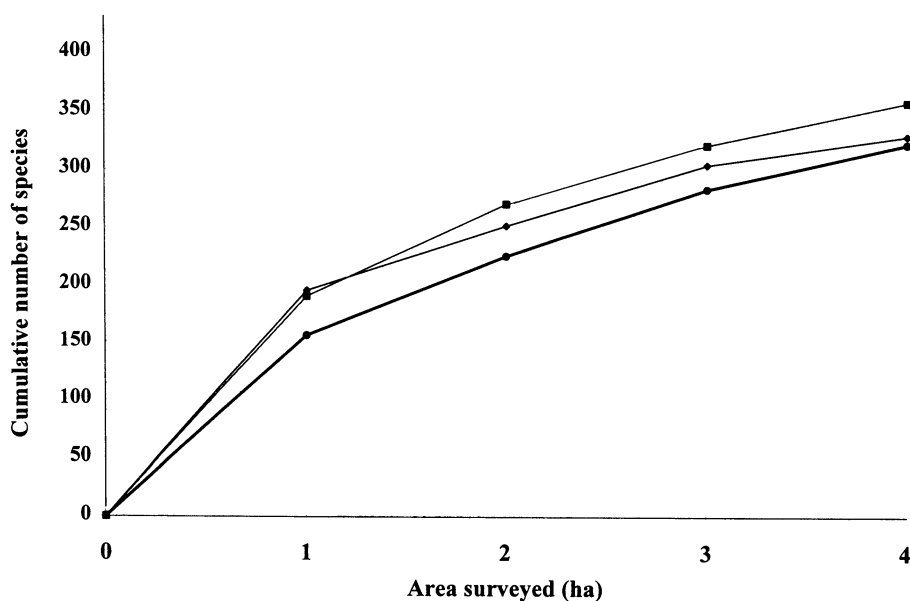


Figure 4. Species–area curve in the three undisturbed forest plots (4 ha each)

The Shannon index H' for the three control plots was 8.0 and the equitability 0.88 ($H_{\text{max}} = 9.07$). H' indices and the equitabilities calculated in each plot were very similar (plot 1 $H' = 7.54$ & $E = 0.90$, plot 4 $H' = 7.57$ & $E = 0.89$, plot 10 $H' = 7.36$ & $E = 0.88$). More than 70% of the species (i.e. 394 taxa) were recorded with a density equal or lower than one stem per ha ($n \leq 12$ for the overall 12-ha area). Roughly 22% of the species (i.e. 117 taxa) were recorded only once whereas half of the total tree population was represented by 72 taxa.

The commonest species recorded in the primary forest was *Elateriospermum tapos* (Euphorbiaceae) with a mean density of 16 stems ha^{-1} which represented only 3% of the total tree density in the three control plots. The second and third ranked species were *Diospyros endertii* (Ebenaceae, $n = 9$ trees ha^{-1} and 1.7% of the total tree density) and *Madhuca* sp. 2 (Sapotaceae, $n = 8$ trees ha^{-1} and 1.6% of the total tree density). The first dipterocarp, *Shorea parvifolia*, was ranked fourth ($n = 7.8$ trees ha^{-1} or 1.5% of the total density).

The plots shared 153 species in common, comprising 58.3% ($n = 3650$ trees) of the total tree population but only 28% of the total taxa were recorded in the plots. The most similar plots in terms of species composition were 1 and 4 (Jaccard's coefficient $J_{14} = 0.53$, 239 common species). Plot 10 was different from the other two plots ($J_{10-1} = 0.40$, $J_{10-4} = 0.41$ sharing respectively 186 and 199 species with plots 1 and 4).

Dipterocarp richness and composition

In the three control plots, Dipterocarpaceae and Euphorbiaceae, with 61 species each, were the richest families (Table 3). The dominance of dipterocarps in the density and basal area was therefore also recorded in term of species richness. On average, 29 species of dipterocarps ha^{-1} were recorded in primary forest, ranging from 20 to 41 species ha^{-1} . In the three control plots, the most abundant and richest dipterocarp genera were *Shorea* (31 species and 61 stems ha^{-1}), *Dipterocarpus* (12 species and 30 stems ha^{-1}), *Vatica* (8 species and 19 stems ha^{-1} , Figure 5). These three genera comprised 88 and 68% of the dipterocarp tree population and species in the undisturbed forest plots respectively. The commonest dipterocarps species recorded ($n \geq 5$ stems ha^{-1}) were *Shorea parvifolia*, *Dipterocarpus acutangulus*, *S. pinanga* and *S. hopeifolia*. In plot 10, the dominant dipterocarp species was *Parashorea mythiesii* (9% of the total dipterocarp density in the plot) a light-demanding and fast-growing species. In contrast, this species in the other two plots was recorded in much lower density (1% and 2% of the dipterocarp density respectively in plots 1 and 4). The lowest dipterocarp species richness was recorded in plot 10 exhibiting 39 species against 49 and 46 in plots 1 and 4 respectively (cf. Annex 1). Comparison of dipterocarp species composition between the three plots with Jaccard's coefficient showed that as for the overall population, plots 1 and 4 were very similar ($J_{14} = 0.69$ and 39 species in common) whereas plot 10 was different from the other two plots ($J_{10-1} = 0.51$, $J_{10-4} = 0.52$, with respectively 31 and 29 species in common with 1 and 4). In contrast with the other two plots and beside its different topography and soil feature, plot 10 exhibited also big gaps where pioneer species were recorded (*Macaranga hypoleuca* $n = 31$, *M. gigantea* $n = 3$, *M. pruinosa* $n = 4$). The data on forest dynamics during the period 1989–1994 showed that gap formation in plot 10 occurred more often than in the other two plots (unpublished data).

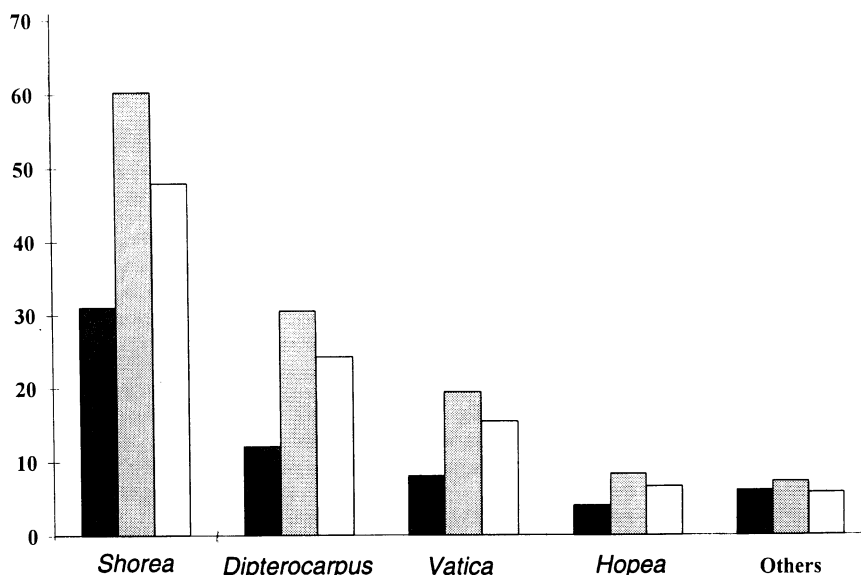


Figure 5. Species richness (number of species, hatched bars), density (stems ha⁻¹, dotted bar) and proportion of the main dipterocarp genera (% of all dipterocarps density, empty bars) in the three control plots (12 ha). Others include : *Anisoptera costata*, *A. laevis*, *Cotylelobium melanoxyton*, *Dryobalanops beccarii*, *Parashorea malaanonan* and *P. smythiesii*.

The genus *Shorea*, which is one of the most demanded for timber, includes several commercial groups known by Indonesian foresters as red meranti, white meranti, yellow meranti and balau. In the primary forest, red meranti, the highest quality timber within the genus, were dominant (52% of the *Shorea* density) followed by yellow meranti (24%) and balau (20%) which showed similar densities. In contrast, white meranti were very few and represented only 4% of the genus density.

Discussion and conclusion

The data presented in Table 4 demonstrate the considerable variations in both stem density and basal area among the lowland mixed dipterocarp forests in Borneo. Tree density and basal area of the Berau forest were very similar to those recorded in Brunei at Belalong by Poulsen *et al.* (1996, in Davies & Becker 1996) and at Ladan by Davies and Becker (1996), and in East Kalimantan at Wanariset by Kartawinata *et al.* (1981). Tree density and basal area (521 stems ha⁻¹ and 30 m² ha⁻¹) were much lower than those recorded by Nicholson (1965) in Sandakan, Sabah (608 trees ha⁻¹ and 42 m² ha⁻¹) and in Sarawak (G. Mulu, Proctor *et al.* 1983, and Lambir 3,4,5, Philips *et al.* 1994, Table 4). However, proportions of dipterocarps in stem density (25.5%) and basal area (50%) were similar to those recorded by Nicholson (1965) in Sabah where dipterocarps comprised 27% of the tree density, and in Sarawak, ha⁻¹ in Gunung Mulu National Park, where Proctor *et al.* (1983) recorded 120 dipterocarps ha⁻¹ comprising 49% of the total basal area (Table 4).

Table 4. Species richness, stem density and basal area for trees ≥ 9.5 , 9.7 or 10 cm dbh in primary lowland dipterocarp forest in Borneo (updated from Davies and Becker 1996)

Site	Altitude (m)	Soil	Plot size (ha)	Species (ha ⁻¹)	No. trees (ha ⁻¹)	% dipt. (ha ⁻¹)	Basal area (m ² ha ⁻¹)	% Dipt. basal area	Reference
Sarawak									
G. Mulu	200	Red-Yellow Podsol	0.95	214+	778	16.2	57	49.1	Proctor <i>et al.</i> (1983)
Lambir 2	114	Clay Udult	0.6	212*	462	-	43	-	Phillips <i>et al.</i> (1994)
Lambir 3,4,5	114	Sandy Humult	3 \times 0.6	240*	739	-	53	-	Phillips <i>et al.</i> (1994)
Brunei									
Belalong	250	Shale-derived Acrisol	1.0	231	550	-	41	-	Poulsen <i>et al.</i> (1996)
Ladang	70	Haplic Acrisol	0.96	194+	500	18 [‡]	40	56 [‡]	Davies & Becker (1996)
Andulau	60	Sandy Haplic Acrisol and Dystric Acrisol	0.96	256+	621	9 [‡]	35	32 [‡]	Davies & Becker (1996)
Sabah									
Sepilok-RP 17	30	Red-yellow Podsol	1.8	157	666	27	42	-	Nicholson (1965)
Danum Valley	60	Haplic Acrisol & Dystric Cambisols	2 \times 4	130	470	16	27	49	Newberry <i>et al.</i> (1992)
East Kalimantan									
Lempake	40-80	Red-yellow Podsol	1.6	167*	445	6	34	39	Riswan (1987)
Kutai	338	Red-yellow Podsol	6 \times 0.8	-	-	-	43	24	Suselo & Riswan (1987)
Wanariset	50	Red-yellow Podsol	1.6	174	541	16	30	55	Kartawinata <i>et al.</i> (1981)
Berau	<100	Hapludult & Paleudult	3 \times 4	182*	521 [†]	25 [†]	31 [†]	50 [†]	This paper

+ = observed number of species in plots slightly smaller than 1 ha

* = estimated made from interpretation of species-area curve

@ = mean number of species calculated on 12 unit squares of 1 ha each (3 plots, 4 ha each)

† = mean of 12 unit squares, 1 ha each (3 plots, 4 ha each)

‡ = from dbh ≥ 5 cm

The forest of Berau is dominated by Dipterocarpaceae and Euphorbiaceae which comprised 37% of the total tree density and 57% of the basal area. More than 70% of the species were recorded with a density lower or equal to one stem per ha but this pattern of low species density is commonly reported in tropical rain forests (Proctor *et al.* 1983, Whitmore, 1984, Gentry 1989, Phillips *et al.* 1994). In the study area, on average, 182 tree species (dbh \geq 10 cm) ha⁻¹ were recorded in the three control plots (12 ha). This species richness is very similar to that commonly found in other parts of Borneo which is generally close to 200 species ha⁻¹. The Dipterocarpaceae and Euphorbiaceae families, each with 61 species or 29 species ha⁻¹, were the richest taxa. Before logging, in the 12 plots totalling 48 ha, 74 species of dipterocarps were recorded. In comparison, Nicholson (1965), in Sabah, reported 198 tree species including 21 dipterocarps in a 1.9-ha plot. In East Kalimantan, Kartawinata *et al.* (1981) counted 239 species (14 dipterocarps) in a 1.6-ha plot. In Sabah (Danum Valley), Newbery *et al.* (1992) recorded 247 species in a 2-ha plot. In Sarawak, Proctor *et al.* (1983) counted 214 tree species in a 1-ha plot. The forest of Berau is therefore much richer in dipterocarps than the neighbour forests of Sabah which are mainly dominated by light-demanding dipterocarps like *Parashorea* spp. and *Dryobalanops* spp. The higher species richness of the Brunei and Sarawak dipterocarp forest, in comparison with those of Sabah (Table 4), could result from a higher stability of the northwest of Borneo which experienced less dramatic drought periods than the eastern part of the Island (Goldammer *et al.* 1996, Walsh 1996). However, the data from the present study demonstrate that in spite of its eastern location, the forest of Berau has a higher species richness than the forest of Sabah, particularly in dipterocarps. Because of its inland situation (about 75 km from the coast), the STREK area may have experienced less dramatic drought periods than coastal stations in East Kalimantan (Balikpapan, Samarinda and Tanjung Redeb for the study area) or Sabah. The high species richness of the Berau forest could be correlated to a longer stability of this forest which faces less dramatic drought events. However, our knowledge on the floristic variation occurring in Borneo is based on data mainly collected in the northern part of the island (Sabah, Sarawak and Brunei). The first record of *Shorea leptoderma* and *S. symingtonii* for Indonesia in the study area (Sist 1996) demonstrates that botanical surveys in East Kalimantan are still needed to improve our knowledge of the flora of Borneo. The lack of data for Kalimantan is undoubtedly an handicap for the analysis of phytogeographical variations within the region. The hypothesis of a possible impact of climatic variations and particularly of drought events on the species distribution and richness in Borneo must therefore be confirmed by further inventories and research in Kalimantan associated with meteorological data monitoring.

Previous studies in lowland dipterocarp forest reported that species richness and composition could be correlated with soil nutrients, particularly with phosphorus and magnesium concentrations (Ashton 1976, 1989, Baillie *et al.* 1987, Pemadosa & Gunatilleke 1981). In contrast, in Malaysia, on a 18-km² surveyed area, Wong and Whitmore (1970) could not find any significant correlation between species distribution and soil features. In Berau, the species richness of dipterocarps was

higher on well-drained soils with gentle slopes than poorly drained zones with steep relief (Sist 1996). In the study area, floristic variations between plots could be correlated with forest dynamics rather than with soil chemical features. In plot 10, the dominance of light demanding species such as *Parashorea mythiesii* and *Dryobalanops beccarii* is likely the result of a higher rate of canopy opening. The higher occurrence of gap formation in plot 10 might be linked to the steep topography of the plots which favoured tree falling. For this reason, logging operations, by creating gaps, are likely to promote the growth and development of such light-demanding dipterocarps and have therefore important consequences on the future forest composition for the next rotation.

The high commercial value of the Berau forest was earlier demonstrated by the assessment of the harvested volume (47 m³ ha⁻¹ in mean) during logging operations in the area (Bertault *et al.* 1995). This richness is enhanced by the dominance of red merantis which are the chief timber export in Southeast Asia. Ultisols are the dominant soil covering 87% of the study area (Sumaryono 1996). Those soils have a poor nutrient status and the most fertile part is the thin surface layer (Bremen *et al.* 1990). Under these conditions, selective logging associated with a long-term forest management plan remains the most suitable and economic profitable land-use system.

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Annex. List of dipterocarp species identified in the 12 plots (4 ha each) in RKL 4 before logging. Codes: 0: species not recorded in control plots; 1,4, 10: species recorded only in plots 1, 4 and 10 respectively; 3: species recorded in all the 3 plots; 14: species recorded in both plots 1 and 4 only; 101: species recorded in both plots 10 and 1 only; 104: species recorded in both plots 10 and 4 only.

Species	Code
<i>Anisoptera costata</i> Korth.	14
<i>Anisoptera laevis</i> Ridl.	14
<i>Cotylelobium melanoxydon</i> (Hook. f) Slooten	1
<i>Dipterocarpus acutangulus</i> Vesque	14
<i>Dipterocarpus confertus</i> Slooten	3
<i>Dipterocarpus conformis</i> Slooten	0
<i>Dipterocarpus costulatus</i> Slooten	1
<i>Dipterocarpus elongatus</i> Korth.	3
<i>Dipterocarpus glabrigemmatum</i> Ashton	0
<i>Dipterocarpus gracilis</i> Blume	10
<i>Dipterocarpus grandiflorus</i> Blanco	14
<i>Dipterocarpus hasseltii</i> Blanco	0
<i>Dipterocarpus humeratus</i> Slooten	3
<i>Dipterocarpus kunstleri</i> King	10
<i>Dipterocarpus pachyphyllus</i> Meijer	1
<i>Dipterocarpus palembanicus</i> Slooten ssp. <i>borneensis</i> Ashton	14
<i>Dipterocarpus stellatus</i> Vesque ssp. <i>parvus</i> Ashton	1
<i>Dipterocarpus verrucosus</i> Foxw. ex Slooten	3
<i>Dryobalanops beccarii</i> Dyer	101
<i>Hopea bracteata</i> Burck	0
<i>Hopea dryobalanoides</i> Miq.	3
<i>Hopea ferruginea</i> Parijs	4
<i>Hopea nervosa</i> King	0
<i>Hopea pachycarpa</i> (Heim) Symington	3
<i>Hopea sangal</i> Korth.	0
<i>Hopea semicuneata</i> Symington	4
<i>Parashorea malaanonan</i> (Blanco) Merr.	10
<i>Parashorea smythiesii</i> Wyatt-Smith ex Ashton	3
<i>Shorea agamii</i> ssp. <i>agamii</i> Ashton	3
<i>Shorea almon</i> Foxw.	3
<i>Shorea angustifolia</i> Ashton	3
<i>Shorea atrinervosa</i> Symington	3
<i>Shorea beccariana</i> Burck	14
<i>Shorea confusa</i> Ashton	0
<i>Shorea exelliptica</i> Meijer	3
<i>Shorea faguetiana</i> Heim	104
<i>Shorea falciferoides</i> ssp. <i>glaucescens</i> (Meijer) Ashton	0
<i>Shorea fallax</i> Meijer	101
<i>Shorea guiso</i> (Blanco) Blume	0
<i>Shorea hopeifolia</i> (Heim) Symington	3
<i>Shorea inappendiculata</i> Burck	3
<i>Shorea johorensis</i> Foxw.	3
<i>Shorea laevis</i> Ridl.	14
<i>Shorea lamellata</i> Foxw.	104
<i>Shorea leprosula</i> Miq.	3
<i>Shorea leptoderma</i> Meijer	14
<i>Shorea longisperma</i> Roxb.	104
<i>Shorea macrophylla</i> x <i>pinanga</i>	0

continued

Annex (continued)

<i>Shorea macroptera</i> spp. <i>sandakanensis</i> (Symington) Ashton	14
<i>Shorea maxwelliana</i> King	1
<i>Shorea mecistopteryx</i> Ridl.	10
<i>Shorea ochracea</i> Symington	4
<i>Shorea ovalis</i> ssp. <i>ovalis</i> Burck	14
<i>Shorea parvifolia</i> Dyer ssp. <i>parvifolia</i> Ashton	3
<i>Shorea parvifolia</i> Dyer ssp. <i>velutinata</i> Ashton	3
<i>Shorea parvistipulata</i> Heim ssp. <i>albifolia</i> Ashton	3
<i>Shorea parvistipulata</i> Heim ssp. <i>parvistipulata</i> Brandis	3
<i>Shorea patoiensis</i> Ashton	3
<i>Shorea pauciflora</i> King	3
<i>Shorea pinanga</i> Scheff.	3
<i>Shorea scrobiculata</i> Burck	101
<i>Shorea seminis</i> (De Vriese) Slooten	0
<i>Shorea smithiana</i> Symington	3
<i>Shorea superba</i> Symington	101
<i>Shorea symingtonii</i> Wood	0
<i>Shorea virescens</i> Parijs	4
<i>Shorea xanthophylla</i> Symington	0
<i>Vatica albiramis</i> Slooten	10
<i>Vatica micrantha</i> Slooten	3
<i>Vatica nitens</i> King	14
<i>Vatica oblongifolia</i> ssp. <i>multinervosa</i> Hook.f.	3
<i>Vatica odorata</i> (Griff.) Symington ssp. <i>mindanensis</i> (Foxw.) Ashton	14
<i>Vatica rassak</i> (Korth.) Blume	14
<i>Vatica sarawakensis</i> Heim	101
<i>Vatica umbonata</i> (Hook.f.) Burck	3
<i>Vatica vinosa</i> Ashton	3
