An Enumeration of One Hectare of Pantai Aceh Forest Reserve, Penang

IAN TURNER*
Oxford Forestry Institute
Department of Plant Sciences
University of Oxford

Abstract

One hectare of forest in Pantai Aceh F.R. was enumerated for stems >10 cm d.b.h., and to a 1 cm d.b.h. lower limit in a 0.05 ha subplot.

The large plot was found to contain 374 stems belonging to 70 or so species. The Dipterocarpaceae was the most abundant family (34% of stems ≥10 cm d.b.h. *Shorea curtisii* dominated the largest size class (>30 cm d.b.h.) with 48 out of 81 stems. The most numerous species in the sub-canopy were: *Shorea maxwelliana, Porterandia anisophylla* and *Pternandra coerulescens*.

The floristic composition indicates that Pantai Aceh is a coastal hill dipterocarp forest of the *Shorea curtisii-Eugeissona tristis* segregate.

Analyses of stand tables, together with the known history of logging on the site, lead to the conclusion that the composition of the forest is changing. More shade-tolerant dipterocarp species such as *Shorea maxwelliana* are taking over the upper canopy as *Shorea curtisii* fails to regenerate.

Introduction

Investigations into the seedling ecology of tree species in Pantai Aceh Forest Reserve, Penang, Peninsular Malaysia (Turner 1988) made it evident that there were considerable differences in the demography of seedlings of various *Shorea* species. *Shorea curtisii* seedlings showed a very high mortality in their first year (93%), significantly higher than in the more shade-tolerant *Shorea multiflora* (72%). It was therefore decided to look in detail at a small area of forest to see if these differences in present-day regenerative capability were reflected in the composition and structure of the forest.

Materials and Methods

One hectare of forest on the east-facing hillside behind the Muka Head Field Station of Universiti Sains Malaysia was enumerated in November 1987. A 100 m × 100 m square was marked out by walking on a bearing for 100 metres, then on a perpendicular bearing for another 100 m and so on. The end of the fourth side was some 10 m out from the starting point; to compensate for this the line was angled in from the 70 m point on this fourth side. The plot is, therefore, only an approximation for one hectare.

* Present Address: Department of Botany, National University of Singapore, Lower Kent Ridge Road, Singapore 0511.

All trees within the plot were measured for girth at breast height and those 32 cm or greater (i.e. ≥10 cm d.b.h.) were tagged and identified as far as possible by using binoculars and collecting and matching fallen leaves.

In addition on five 10 m × 10 m sub-plots along the lower edge from the north-east corner all stems of 1 cm d.b.h. or greater were enumerated and all dipterocarp seedlings were tagged and measured for height.

Results

A total of 374 stems with d.b.h. ≥10 cm were recorded from the 1 ha plot; comprising some 65 recognised, but not in all cases named, species (Table 1). Twenty-six stems remained indetermined because no distinguishing features could be seen from the ground so the appropriate fallen leaves could not be picked out from the litter. This group may contain up to ten extra species, but five or six is probably a fairer estimate, thus giving an overall species count of approximately seventy.

The forest is dominated by the Dipterocarpaceae: 34% of all stems greater than 10 cm d.b.h. (see Table 2 and Fig. 1) with the Rubiaceae the next most abundant family with 16%. The Dipterocarpaceae are also represented by the highest number of species, eleven in all. As is usual with tropical rain forests many species are rare (Jacobs 1988, Whitmore 1988), in this case more than two-thirds of the species are represented by under 1% of the total number of stems each.

The nature of the forest is elucidated by breaking down the results by size class (Class 1 = 1–10 cm d.b.h., Class 2 = 10.1–20 cm d.b.h., Class 3 = 20.1–30 cm d.b.h. and Class 4 = >30 cm d.b.h.). Class 4, the canopy-top trees, is dominated by the dipterocarp *Shorea curtisii* with 48 out of 81 stems. *Gluta curtisii* (Anacardiaceae) is the only other species to make up more than 10% of the total in this class.

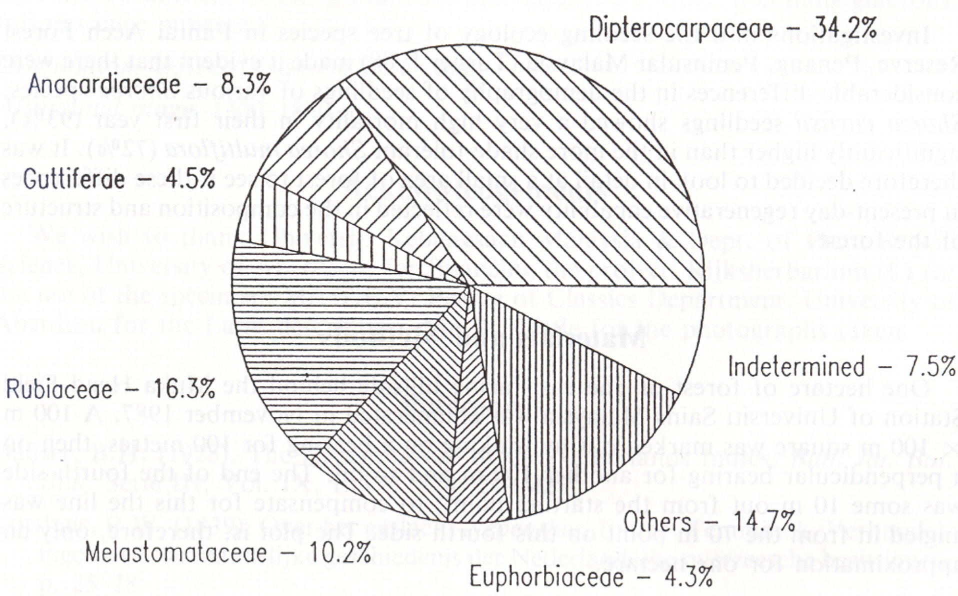

Fig. 1. Relative abundance of families for all stems >10 cm d.b.h. on 1 ha of forest in Pantai Aceh F.R., Penang.

Table 1

A list of the tree species found on 1 ha of hill forest in Pantai Aceh F.R.
(Class 2: 10.1–20 cm d.b.h., Class 3: 20.1–30 cm d.b.h., Class 4: >30 cm d.b.h.)

Species	Family	Class 2	Class 3	Class 4	TOTAL
Shorea curtisii Dyer ex King	Dipterocarpaceae	1	2	48	51
Shorea maxwelliana King	Dipterocarpaceae	31	18	1	50
Porterandia anisophylla (Jack ex Roxb.) Ridley	Rubiaceae	37	3	—	40
Pternandra coerulescens Jack	Melastomataceae	38	—	—	38
Gluta curtisii (Oliv.) Ding Hou	Anacardiaceae	4	2	11	17
Timonius corneri K.M. Wong	Rubiaceae	13	1	—	14
Shorea multiflora (Burck) Sym.	Dipterocarpaceae	4	1	2	7
Elaeocarpus sp.	Elaeocarpaceae	6	—	—	6
Glochidion superbum Baill.	Euphorbiaceae	6	—	—	6
Anisoptera curtisii Dyer ex King	Dipterocarpaceae	2	2	1	5
Cryptocarya ferrea Bl.	Lauraceae	4	—	1	5
Gironniera parvifolia Planch.	Ulmaceae	5	—	—	5
Calophyllum calaba L.	Guttiferae	1	—	3	4
Eugenia sp.	Myrtaceae	2	1	1	4
Garcinia sp. A	Guttiferae	3	1	—	4
Gluta aptera (King) Ding Hou	Anacardiaceae	3	—	1	4
Homolanthus populneus (Geisel.) Pax	Euphorbiaceae	2	2	—	4
Swintonia spicifera Hk.f.	Anacardiaceae	3	—	1	4
Austrobuxus nitidus Miq.	Euphorbiaceae	3	—	—	3
Calophyllum teysmannii Miq.	Guttiferae	1	1	1	3
Calophyllum wallichianum Planch. et Triana	Guttiferae	3	—	—	3
Kokoona reflexa (Laws.) Ding Hou	Celastraceae	3	—	—	3
Psydrax sp. 1	Rubiaceae	3	—	—	3
Shorea ovata Dyer ex Brandis	Dipterocarpaceae	—	2	1	3
Shorea sp.	Dipterocarpaceae	—	2	1	3
Vatica sp.	Dipterocarpaceae	2	1	—	3
?311	unknown	3	—	—	3
Artocarpus lowii King	Moraceae	1	1	—	2
Brackenridgea hookeri (Planch.) A. Gray	Ochnaceae	2	—	—	2
Buchanania arborescens (Bl.) Bl.	Anacardiaceae	—	2	—	2
indet.	Burseraceae	2	—	—	2
Calophyllum molle King	Guttiferae	2	—	—	2
Dacryodes longifolia (King) Lam	Burseraceae	2	—	—	2
Dillenia grandifolia Wall. ex Hk.f. et Thoms.	Dilleniaceae	—	1	1	2
Elaeocarpus ferrugineus Steud.	Elaeocarpaceae	2	—	—	2
Eugenia attenuata (Miq.) Koord. & Val.	Myrtaceae	1	1	—	2

Table 1 *(cont'd)*

Species	Family	Class 2	Class 3	Class 4	TOTAL
Gardenia tubifera Wall.	Rubiaceae	2	—	—	2
Gluta elegans Kurz	Anacardiaceae	2	—	—	2
Hopea pedicellata (Brandis) Sym.	Dipterocarpaceae	2	—	—	2
indet.	Lauraceae	1	1	—	2
Lithocarpus wallichianus (Lindl. ex Hance) Rehd.	Fagaceae	—	2	—	2
Ryparosa sp.	Flacourtiaceae	2	—	—	2
Symplocos adenophylla Wall. ex Don	Symplocaceae	2	—	—	2
Rengas sp.	Anacardiaceae	1	—	—	1
Aporusa benthamiana Hk.f.	Euphorbiaceae	1	—	—	1
Artocarpus sp.	Moraceae	—	—	1	1
Bhesa paniculata Arn.	Celastraceae	—	—	1	1
Buchanania sessifolia Bl.	Anacardiaceae	1	—	—	1
Canarium littorale Bl.	Burseraceae	1	—	—	1
Canarium sp.	Burseraceae	—	—	1	1
Canthium confertum Korth.	Rubiaceae	1	—	—	1
Dacryodes rugosa (Bl.) Lam	Burseraceae	1	—	—	1
Dipterocarpus caudatus Foxw.	Dipterocarpaceae	—	1	—	1
Dipterocarpus grandiflorus (Blanco) Blanco	Dipterocarpaceae	1	—	—	1
Drypetes sp.	Euphorbiaceae	1	—	—	1
Garcinia sp. B	Guttiferae	1	—	—	1
Gordonia penangensis Ridley	Theaceae	1	—	—	1
Heritiera sumatrana (Miq.) Kosterm.	Sterculiaceae	1	—	—	1
Hopea beccariana Burck	Dipterocarpaceae	—	—	1	1
Mallotus sp.	Euphorbiaceae	1	—	—	1
indet.	Myristicaceae	1	—	—	1
Payena obscura Burck	Sapotaceae	1	—	—	1
indet.	Rosaceae	1	—	—	1
indet.	Rubiaceae	1	—	—	1
Schoutenia accrescens (Mast.) Curtis	Tiliaceae	1	—	—	1
Indetermined		20	3	3	26
TOTAL		242	51	81	374
(Total number spp identified)		(56)	(21)	(18)	(65)

Table 2
The families of trees found on 1 ha of coastal hill dipterocarp forest (stems >10 cm d.b.h.)

Family	Number of stems	Species per Family
Dipterocarpaceae	128	11
Rubiaceae	61	6
Melastomataceae	38	1
Anacardiaceae	31	7
Guttiferae	17	6
Euphorbiaceae	16	5
Burseraceae	7	6
Elaeocarpaceae	7	2
Lauraceae	7	2
Myrtaceae	6	1
Ulmaceae	5	1
Celastraceae	4	2
Moraceae	3	3
Dilleniaceae	2	1
Fagaceae	2	1
Flacourtiaceae	2	1
Ochnaceae	2	1
Symplocaceae	2	1
Myristicaceae	1	1
Rosaceae	1	1
Sapotaceae	1	1
Sterculiaceae	1	1
Theaceae	1	1
Tiliaceae	1	1
Indetermined	28	—
TOTAL	374	

The subcanopy has a markedly different composition, with *Shorea maxwelliana, Porterandia anisophylla* (Rubiaceae) and *Pternandra coerulescens* (Melastomataceae) being the commonest species. This is reflected in the familial composition of Class 2 (Fig. 2) with the Rubiaceae the most abundant (22.5%) followed by the Dipterocarpaceae (17%) and the Melastomataceae (15%). *Porterandia anisophylla* is common in the small gaps formed in the canopy where the large trees die standing. Raich (1987) has shown that *Porterandia anisophylla* is restricted to canopy gaps at Pantai Aceh and that its seeds germinate better in a small gap compared to a closed-canopy site or large clearing.

The stand table for *Shorea curtisii* (Fig. 3) is heavily skewed to the biggest size

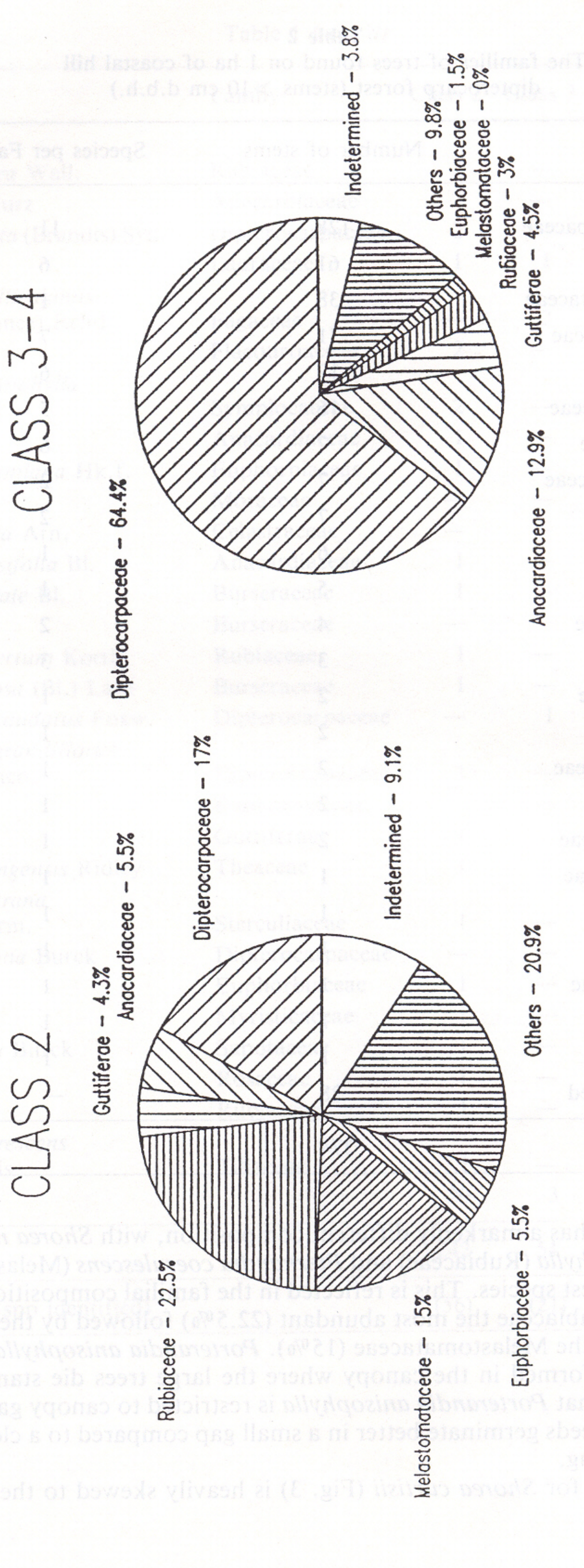

Fig. 2. Relative abundances of families in different size classes (Class 2 = 10.1–20 cm d.b.h., Class 3–4 = >20 cm d.b.h.) on 1 ha of forest in Pantai Aceh F.R., Penang.

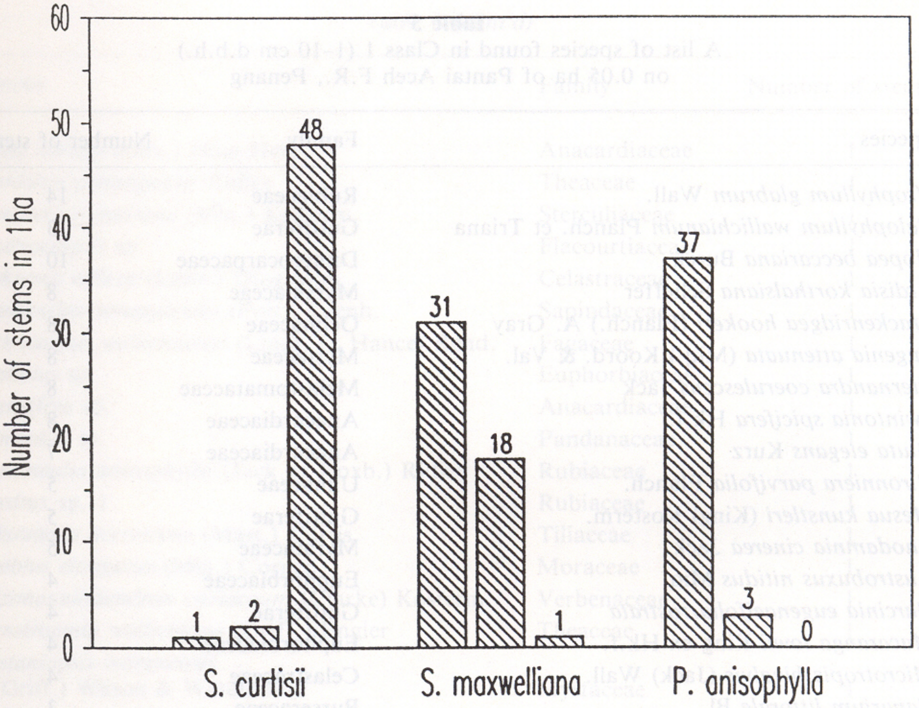

Fig. 3. Stand tables for the three commonest species, *Shorea curtisii, Shorea maxwelliana* and *Porterandia anisophylla* from 1 ha of forest in Pantai Aceh F.R., Penang. Bars from left to right represent Class 2 (10.1–20 cm d.b.h.), Class 3 (20.1–30 cm d.b.h.) and Class 4 (>30 cm d.b.h.).

class whereas *Shorea maxwelliana* has more small trees than large. No individuals of *Porterandia anisophylla* reach the largest size class.

The more detailed enumeration of the 0.05 ha area shows that the understorey, Class 1, has a more mixed composition (Table 3 and Fig. 4), the Guttiferae being the commonest family. In addition to the 190 tree and shrub stems recorded in Class 1 there were 7 stems of rattans and other woody climbers with a d.b.h. greater than 1 cm. Large climbers do not appear to be abundant at Pantai Aceh. There were 62 clumps of the stemless palm, bertam (*Eugeissona tristis* Griff.) in the 0.05 ha area, each with a mean of 6.1 leaves (standard error = 0.5). Only two clumps showed signs of having ever flowered.

The stand table (Fig. 5) for the 0.05 ha shows the usual reverse-J curve of a primary rain forest with many small saplings and fewer large trees. Fig. 6 is a species-area curve for the five 100 m^2 sub-plots for all stems >1 cm d.b.h. The points represent the average of five random compilations of the data from the five sub-plots. The curve is still rising at 500 m^2.

A total of 379 individual seedlings of six species of dipterocarp were recorded from the five 100 m^2 sub-plots (Table 4). The commonest was *Hopea beccariana* which had a greater mean height than the other two common seedlings, *Shorea curtisii* and *Shorea multiflora*. Many of the *Shorea curtisii* seedlings were from the fruiting of September 1986.

Table 3
A list of species found in Class 1 (1–10 cm d.b.h.) on 0.05 ha of Pantai Aceh F.R., Penang

Species	Family	Number of stems
Urophyllum glabrum Wall.	Rubiaceae	14
Calophyllum wallichianum Planch. et Triana	Guttiferae	13
Hopea beccariana Burck	Dipterocarpaceae	10
Ardisia korthalsiana Scheffer	Myrsinaceae	8
Brackenridgea hookeri (Planch.) A. Gray	Ochnaceae	8
Eugenia attenuata (Miq.) Koord. & Val.	Myrtaceae	8
Pternandra coerulescens Jack	Melastomataceae	8
Swintonia spicifera Hk.f.	Anacardiaceae	8
Gluta elegans Kurz	Anacardiaceae	7
Gironniera parvifolia Planch.	Ulmaceae	5
Mesua kunstleri (King) Kosterm.	Guttiferae	5
Rhodamnia cinerea Jack	Myrataceae	5
Austrobuxus nitidus Miq.	Euphorbiaceae	4
Garcinia eugenaeifolia/rostrata	Guttiferae	4
Macaranga lowii King ex Hk.f.	Euphorbiaceae	4
Microtropis bivalvis (Jack) Wall.	Celastraceae	4
Canarium littorale Bl.	Burseraceae	3
Eugenia sp. B	Myrtaceae	3
Shorea curtisii Dyer ex King	Dipterocarpaceae	3
Shorea maxwelliana King	Dipterocarpaceae	3
Shorea ovata Dyer ex Brandis	Dipterocarpaceae	3
Anisophyllea corneri Ding Hou	Rhizophoraceae	2
Ardisia sp.	Myrsinaceae	2
Baccaurea sumatrana (Miq.) M.A.	Euphorbiaceae	2
Calophyllum teysmannii Miq.	Guttiferae	2
Cryptocarya ferrea Bl.	Lauraceae	2
Eurycoma longifolia Jack	Simaroubaceae	2
Garcinia sp.	Guttiferae	2
Guioa fuscidula (Kurz) Radlk.	Sapindaceae	2
Hopea pedicellata (Brandis) Sym.	Dipterocarpaceae	2
Lophopetalum floribundum Wight.	Celastraceae	2
Semecarpus sp.	Anacardiaceae	2
Shorea sp.	Dipterocarpaceae	2
Timonius corneri K.M. Wong	Rubiaceae	2
Aidia cochinchinensis Lour.	Rubiaceae	1
indet.	Annonaceae	1
Arthrophyllum diversifolium Bl.	Araliaceae	1
Barringtonia macrostachya (Jack) Kurz	Lecythidaceae	1
Buchanania sessifolia Bl.	Anacardiaceae	1
Dacryodes longifolia (King) Lam	Burseraceae	1
Eugenia sp. A	Myrtaceae	1
Garcinia malaccensis/penangiana	Guttiferae	1
Gluta aptera (King) Ding Hou	Anacardiaceae	1

Table 3 *(cont'd)*

Species	Family	Number of stems
Gluta curtisii (Oliv.) Ding Hou	Anacardiaceae	1
Gordonia penangensis Ridley	Theaceae	1
Heretiera sumatrana (Miq.) Kosterm.	Sterculiaceae	1
Hydnocarpus sp.	Flacourtiaceae	1
Kokoona reflexa (Laws.) Ding Hou	Celastraceae	1
Lepisanthes senegalensis (Poir.) Leenh.	Sapindaceae	1
Lithocarpus wallichianus (Lindl. ex Hance) Rehd.	Fagaceae	1
Mallotus sp.	Euphorbiaceae	1
Mangifera sp.	Anacardiaceae	1
Pandanus sp.	Pandanaceae	1
Porterandia anisophylla (Jack ex Roxb.) Ridley	Rubiaceae	1
Psydrax sp. 1	Rubiaceae	1
Schoutenia accrescens (Mast.) Curtis	Tiliaceae	1
Streblus elongatus (Miq.) Corner	Moraceae	1
Teijsmanniodendron coriaceum (Clarke) Kosterm.	Verbenaceae	1
Ternstroemia wallichiana (Griff.) Engler	Theaceae	1
Tristaniopsis merguensis (Griff.) Wilson & Waterhouse	Myrtaceae	1
Vatica sp.	Dipterocarpaceae	1
Indetermined		4
TOTAL		190
Lianas and rattans		7

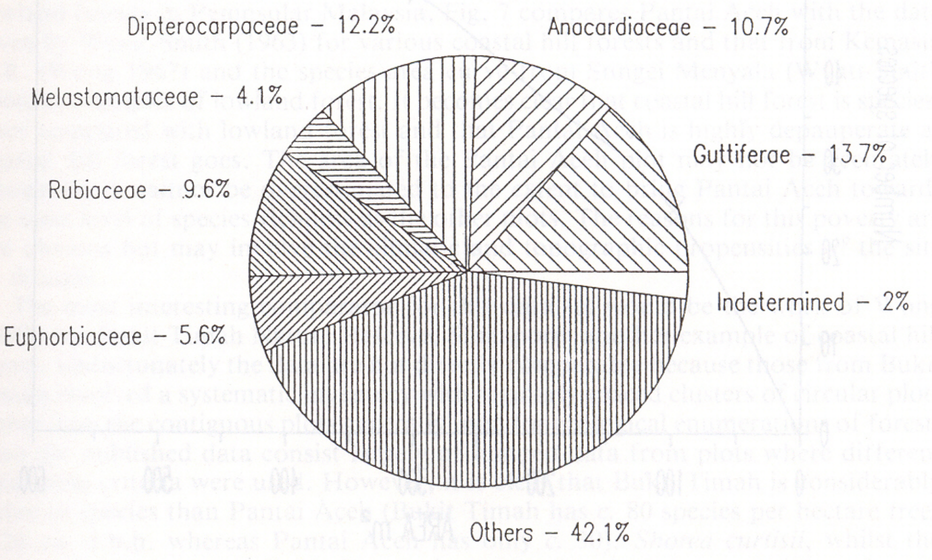

Fig. 4. Relative abundance of families in Class 1 (1–10 cm d.b.h.) from 0.05 ha of forest in Pantai Aceh F.R., Penang.

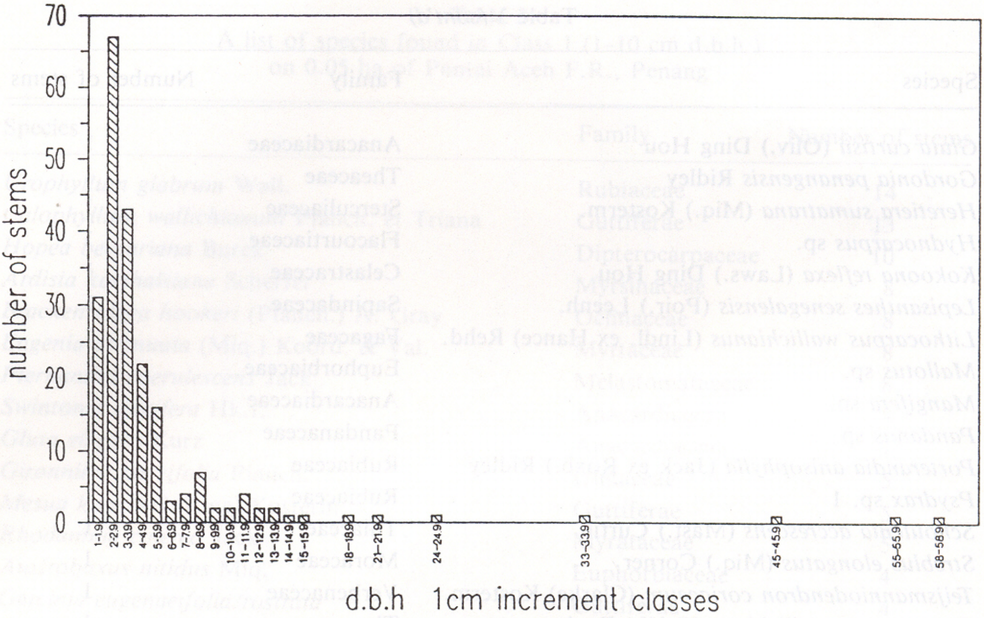

Fig. 5. Stand table for all stems >1 cm d.b.h. on 0.05 ha of forest in Pantai Aceh, F.R., Penang.

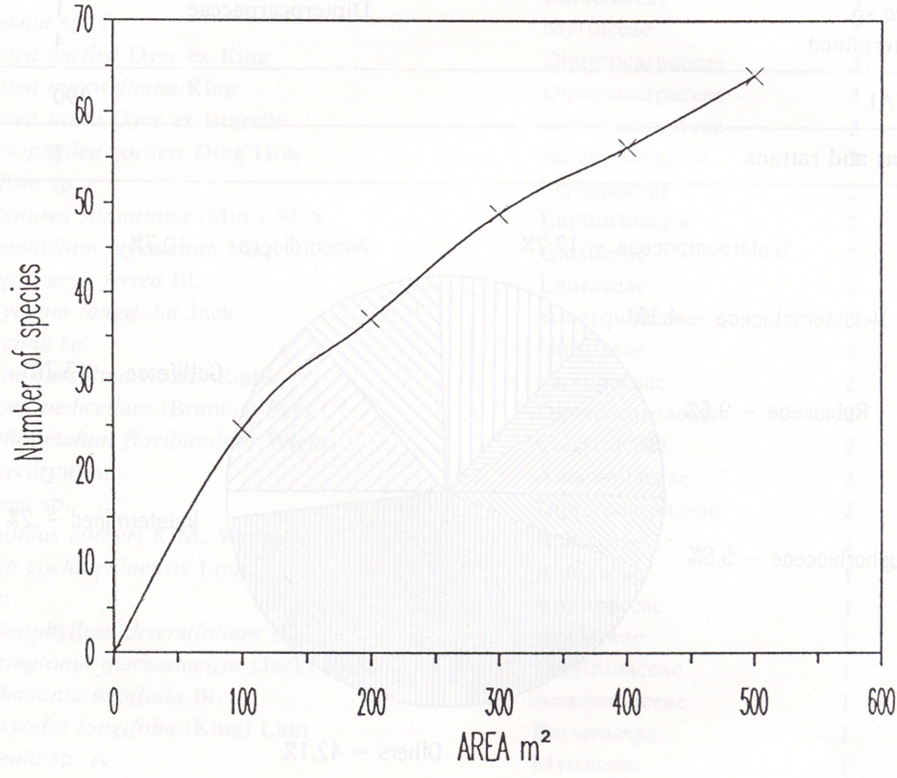

Fig. 6. Species-Area curve for all stems >1 cm d.b.h. from 0.05 ha of forest in Pantai Aceh, F.R., Penang.

Table 4
The numbers and heights of dipterocarp seedlings
(<1 cm d.b.h.) on 0.05 ha of forest

Species	No. indivs	mean height ± s.e. (cm)
Hopea beccariana	124	74 ± 7
Shorea curtisii	108	30 ± 3
Shorea multiflora	100	22 ± 2
Shorea maxwelliana	30	82 ± 9
Hopea pedicellata	2	157 ± 86
TOTAL	379	

Discussion

The enumeration has shown that the forest at Pantai Aceh is made up of *Shorea curtisii* with some *Gluta curtisii*, overtopping a subcanopy of *Shorea maxwelliana, Pternandra coerulescens* and various other Rubiaceous and some Euphorbiaceous trees; with *Porterandia anisophylla* being common in the small canopy gaps. The understorey is rife with bertam; with tree seedlings and saplings, mostly those of dipterocarp species, occupying the spaces between the clumps. The floristic composition is clearly that of the subformation of coastal hill forest known as the *Shorea curtisii-Eugeissona* association-segregate as defined by Symington (1943) which was later called seraya-ridge-forest (Wyatt-Smith 1963). Wyatt-Smith (1963) pointed to *Anisoptera curtisii, Calophyllum teysmannii* var. *inophylloide, Calophyllum wallichianum, Hopea beccariana* and *Shorea multiflora* as species characteristic of this subformation. They are all common at Pantai Aceh.

In general Pantai Aceh comes out as being species-poor in comparison with other lowland forests in Peninsular Malaysia. Fig. 7 compares Pantai Aceh with the data given by Wyatt-Smith (1963) for various coastal hill forests and that from Kemasul F.R. (Wong 1967) and the species-area curve from Sungei Menyala (Wyatt-Smith 1966) as examples of lowland forest. It becomes clear that coastal hill forest is species-poor compared with lowland forest and that Pantai Aceh is highly depauperate as coastal hill forest goes. The area of the Pantai Aceh plot may not be accurately known but it cannot be overestimated to the extent to bring Pantai Aceh towards the same level of species-richness as the other plots. The reasons for this poverty are not obvious but may involve the climatic and topographic propensities of the site to drought.

The most interesting comparator for this data set would be the work of Wong (1987) for Bukit Timah Nature Reserve, Singapore; another example of coastal hill forest. Unfortunately the data are not directly comparable because those from Bukit Timah involved a systematic inventory with regularly spaced clusters of circular plots rather than the contiguous plots generally used for ecological enumerations of forest. Also the published data consist largely of lumped data from plots where different measuring criteria were used. However, it is clear that Bukit Timah is considerably richer in species than Pantai Aceh (Bukit Timah has *c.* 80 species per hectare trees ≥20 cm d.b.h. whereas Pantai Aceh has only *c.* 30). *Shorea curtisii*, whilst the commonest large tree at Bukit Timah, is not as abundant there as at Pantai Aceh but it is regenerating successfully (Wong & Teo 1978); there are no heavy-hardwood

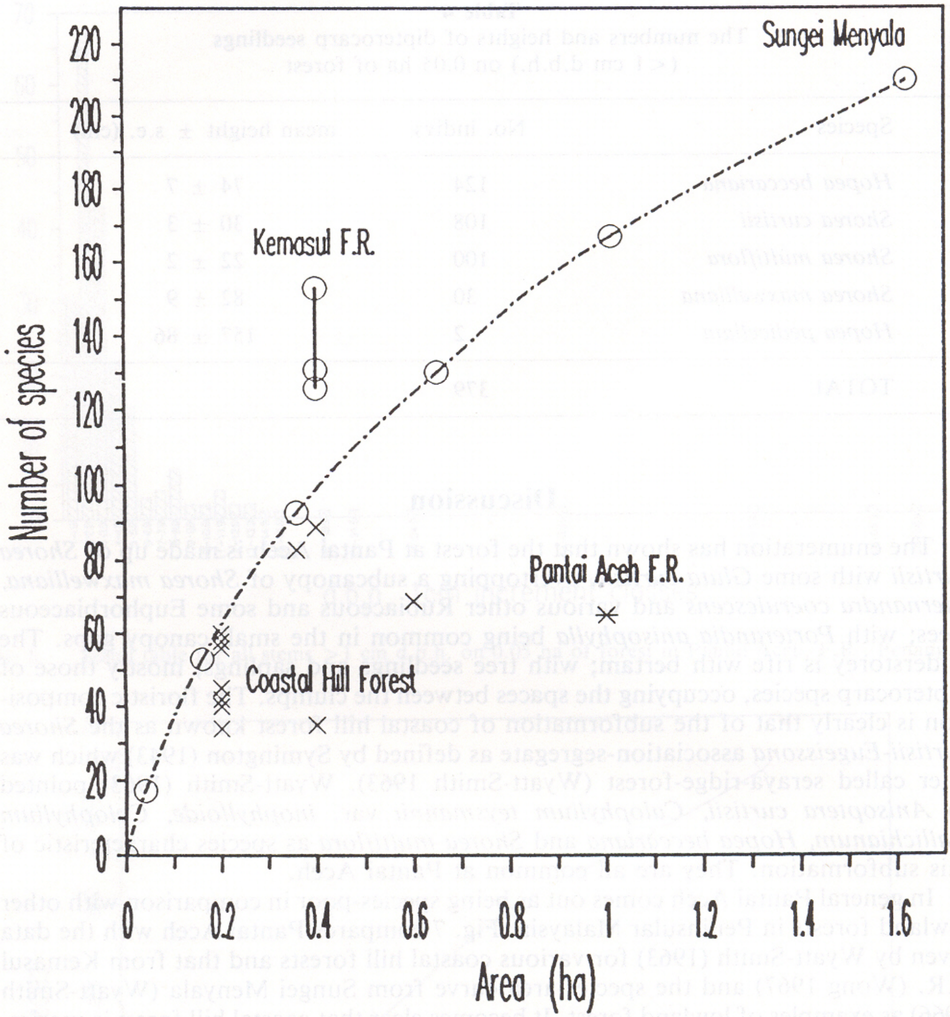

Fig. 7. Species-Area plots for various Malayan forests. Data from Pulau Jarak, Pulau Rumbia, Pulau Pangkor, Kampong Gajah F.R., Banang F.R., Soga F.R., Gunung Raya F.R. and Bukit Enggang F.R, (Wyatt-Smith 1963); Sungei Menyala F.R. (Wyatt-Smith 1966) and Kemasul F.R. (Wong 1967).

Shorea species i.e. the Balau group (*Shorea* section *Shorea*) such as *Shorea maxwelliana*, and the Euphorbiaceae rather than the Rubiaceae dominate the understorey.

The most notable points to come out of the Pantai Aceh data concern comparisons between the stand tables of the two common dipterocarps, *Shorea curtisii* and *Shorea maxwelliana. Shorea curtisii* exhibits a stand table with few middle-sized trees compared to the canopy-top individuals whereas *Shorea maxwelliana* has few big trees and many small ones. A regeneration sampling carried out in Compartment 6 of Pantai Aceh in 949 (Wyatt-Smith 1963) also showed a difference in stand structure between dipterocarp species, though different sizes were considered. A milliacre sampling technique was used which included all trees ≤one foot g.b.h. (*c.* 10 cm d.b.h.). The results are plotted in Fig. 8 with the individuals divided into four size

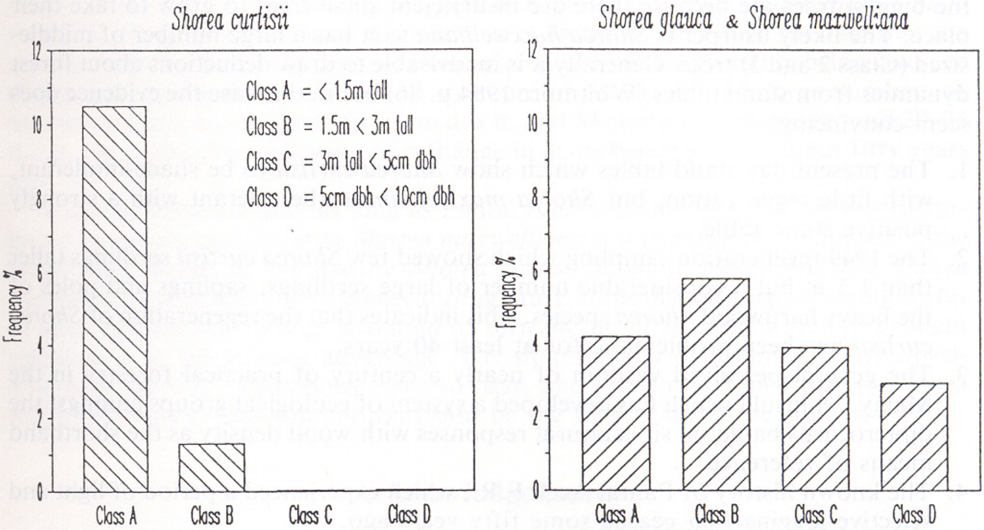

Fig. 8. Results of a linear regeneration sampling of Pantai Aceh F.R. in 1949 (from Wyatt-Smith 1963).

classes. The two heavy hardwood *Shorea* species, *Shorea glauca* and *Shorea maxwelliana*, were well represented in the advanced regeneration of large seedlings, saplings and poles while *Shorea curtisii*, a light hardwood, had many small seedlings but very few individuals in the larger size classes.

Foresters generally regard the wood density of dipterocarps as a reflection of their relative regeneration capabilities or 'tolerance'. Those of a high density, the heavy hardwoods, are known to be very shade tolerant as juveniles; persisting and growing at lower radiation levels than the light hardwood species e.g. as Becker (1983) found in a comparison of *Shorea maxwelliana* and *Shorea leprosula* seedlings in Pasoh F.R., Peninsular Malaysia. Silviculturally this means that the light hardwoods require greater canopy opening (disturbance) to release the seedlings from the suppressed state in the deeply shaded forest understorey than the heavy hardwoods, but respond more rapidly when released (Whitmore 1984).

At present there is more demand for light hardwood timber but in the past, before the advent of chemical wood-preservatives, the heavy hardwoods found greater favour. As Curtis (1894) wrote in the first flora of Penang:

> "*Shorea utilis* King [*Shorea maxwelliana*] 'Damar laut No[mbor] satu' Undoubtedly the best timber in the island [Penang]. Waterfall and Muka Head, too much in demand to be common".

The naturally strong and durable timbers of the Balau group were put to many uses especially heavy structural work such as bridge-building (Desch 1941). Pantai Aceh was exploited for its heavy hardwoods from around 1915 (and probably before) to the late 1930s (Ong & Dhanarajan 1976); though felling of such timber for boat-building may have been going on long before this (J. Wyatt-Smith pers. comm.). The large Balau trees were felled selectively and dragged out by man or buffalo. A few signs of this activity are still evident in the forest in the very occasional tree stump or gully caused by the erosion of a drag line.

It would appear from the stand tables that Pantai Aceh is in a state of compositional change; that *Shorea curtisii* will be unable to replace itself in the canopy as the biggest trees die because there are insufficient small trees to grow to take their place. The likely usurper is *Shorea maxwelliana* as it has a large number of middle-sized (Class 2 and 3) trees. Generally it is inadvisable to draw deductions about forest dynamics from stand tables (Whitmore 1984 p. 86) but in this case the evidence does seem convincing.

1. The present day stand tables which show *Shorea curtisii* to be shade-intolerant, with little regeneration, but *Shorea maxwelliana* to be tolerant with a strongly positive stand table.
2. The 1949 regeneration sampling which showed few *Shorea curtisii* seedlings taller than 1.5 m but a considerable number of large seedlings, saplings and poles of the heavy hardwood *Shorea* species. This indicates that the regeneration of *Shorea curtisii* has been problematic for at least 40 years.
3. The general perceived wisdom of nearly a century of practical forestry in the Malay Peninsula which has developed a system of ecological groups amongst the dipterocarps based on silvicultural responses with wood density as the shorthand means of reference.
4. The known history of Pantai Aceh F.R., which experienced a period of light and selective logging that ceased some fifty years ago.

A hypothesis must be put forward to answer the questions: How did *Shorea curtisii* come to dominate the forest?, and; why did it regenerate successfully in the past but fail to do so now?

The hypothesis presented here is built upon an understanding of the ecologies of these two species (species groups) whose main difference lies in their responses to canopy disturbance via the effects of understorey light levels. Whilst there are no reports of major changes in the frequencies of fierce storms or other cataclysmic natural phenomena there has, as has been stated above, been a change in anthropogenic interference in that the selective felling of heavy hardwood species stopped approximately fifty years ago. It can be hypothesised that the logging activities would have produced canopy disturbance of a magnitude great enough to produce rapid growth of the light hardwood species such as *Shorea curtisii*; which would have been favoured over other light hardwoods because of its probable drought-tolerance (Whitmore 1984) on the steep hillsides of Pantai Aceh (90% of the forest is on slopes of more than 18° (Ong & Dhanarajan 1976)) with their coarse, granite-derived soils. It would seem reasonable to deduce that the present abundance of *Shorea curtisii* is the result of the pre-war selective felling of heavy hardwoods which both selected against these species at maturity and gave the competitive advantage at the juvenile stages to the light hardwoods because of increased illumination of the forest floor. The cessation of logging would have reduced this artificial selection in favour of *Shorea curtisii*. The canopy would have closed over and the average solar radiation levels on the forest floor would fall, favouring the shade-tolerant heavy hardwoods (mostly *Shorea maxwelliana*) over the light hardwoods. Therefore for the last fifty years *Shorea maxwelliana* has successfully regenerated and grown to the small tree size seen today but *Shorea curtisii* has failed because the radiation levels have been too low. Burgess (1975) found that *Shorea curtisii* typically regenerates poorly from seed and that its seedlings do not persist for many years in the shade of the forest understorey. The abundance of bertam at Pantai Aceh, the proliferation of which would also be favoured by logging, may also be deleterious to *Shorea curtisii* regeneration, as Burgess showed in the hill forests he studied. Symington, in his seminal work on the dipterocarps of the Malay Peninsula (1943), gives figures for the mean annual girth increment of the two species; that for *Shorea curtisii* he gives as 1.54 inches year^{-1} and for *Shorea maxwelliana* as 0.92 inches year^{-1}. Therefore in fifty years a tree of *Shorea curtisii* could grow to 60 cm d.b.h. but *Shorea maxwelliana* would be some 40% smaller in diameter, at *c.* 35 cm d.b.h. Given the fact that the growth rates on the drought-prone Penang coastal hills are probably below average (Symington 1943), the present stand structure of the forest with large numbers of *Shorea curtisii* stems around 40–50 cm d.b.h. and *Shorea maxwelliana* around 20–25 d.b.h. are a plausible reflection of a change in disturbance pattern about fifty years ago.

It can be predicted that as long as Pantai Aceh remains in a state of low disturbance frequency and intensity *Shorea maxwelliana* will increase in abundance in the largest size classes as the mature *Shorea curtisii* stand senesces. Possibly *Shorea curtisii* may maintain some presence through rare, large disturbances allowing waves of new regeneration. It may also hold its own on the ridge crests where its drought tolerance is at the greatest advantage. The simplest way of testing this hypothesis will be to see if its predictions come to pass, and it is to be hoped that the forest will be allowed to develop naturally and be the subject of future studies.

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