TREE GROWTH IN PRIMARY LOWLAND AND HILL DIPTEROCARP FORESTS

N. Manokaran & K. M. Kochummen

Forest Research Institute Malaysia, Kepong 52109, Kuala Lumpur, Malaysia

Received December 1992

MANOKARAN, N. & KOCHUMMEN, K. M. 1994. Tree growth in primary lowland and hill dipterocarp forests. Information is analysed and summarised on tree growth over long term in 2-*ha* plots in primary lowland dipterocarp forests in Pasoh Forest Reserve (1971-84) and Sungei Menyala Forest Reserve (1947-85), and in primary hill dipterocarp forest in Bukit Lagong Forest Reserve (1949-85). About 64% of trees ≥10 *cm* DBH grew at slow rates around 1 *mm* y^{-1}, and species groups differed in their rates of growth in the following sequence: understorey < main canopy < emergent ≈ pioneers. In the longer-term plots at Sungei Menyala and Bukit Lagong, canopy species (emergent and main canopy) formed 95% of the fastest growing individuals, and light hardwoods 80%. In the Pasoh plots, 77% of the fastest growing individuals were canopy species, and light hardwoods and medium hardwoods were together 80%. In populations of understorey species and hardwoods, generally regarded as slow growers, there were individuals that grew at high rates comparable to that of fast-growing individuals of canopy species. Fast-growing trees of canopy species, especially dipterocarps, are estimated to be as young as 60 years at a size of 30 *cm* DBH.

Key words: Tree growth - rain forest - canopy species - understorey species - pioneers - dipterocarps

MANOKARAN, N. & KOCHUMMEN, K. M. 1994. Tumbesaran pokok di hutan primer dipterokarpa pamah dan hutan bukit dipterokarpa. Maklumat tentang tumbesaran pokok dalam jangka panjang di dalam petak-petak 2 *ha* di hutan primer dipterokarpa pamah di Hutan Simpan Pasoh (1971-84) dan Hutan Simpan Sungai Menyala (1947-85), dan di hutan primer dipterokarpa bukit di Hutan Simpan Bukit Lagong dianalisa dan diringkaskan. Hampir 64% daripada pokok-pokok ≥ 10 *mm* ppd tumbuh pada kadar yang perlahan sekitar 1 *mm tahun*$^{-1}$. Kadar tumbesaran mengikut spesies adalah berbeza seperti mana mengikut urutan berikut: spesies ternaung < silara utama < unggul ≈ perintis. Di petak-petak jangka panjang di Hutan Simpan Sungai Menyala dan Bukit Lagong, spesies silara (unggul dan silara utama), merangkumi 95% daripada pokok-pokok yang cepat tumbesarannya, dan 80% pula terdiri daripada kumpulan kayu keras ringan. Didalam di petak-petak Hutan Simpan Pasoh , 77% daripada individu-individu yang paling cepat tumbesarannya adalah di kalangan spesies silara, dan 80% terdiri daripada kumpulan kayu keras ringan dan sederhana. Dalam populasi spesies ternaung dan kayu keras pada amnya dianggap sebagai tumbuhan yang tumbuh pada kadar yang perlahan, ada di antara individu yang tumbuh padakadar yang lebih cepat berbanding dengan individu yang cepat tumbuh dikalangan spesies silara. Adalah di anggarakan bahawa bagi pokok-pokok spesies silara yang cepat tumbesarannya, terutamanya dipterokarpa, adalah semuda 60 tahun dan mencapai saiz 30 *cm* ppd.

Introduction

Individual trees of ≥ 10 *cm* diameter at breast height (DBH) have been monitored regularly over long term in four 2- *ha* plots in a lowland dipterocarp forest in Pasoh Forest Reserve, and in one 2- *ha* plot each in a lowland dipterocarp forest in Sungei Menyala Forest Reserve and in a hill dipterocarp forest in Bukit Lagong Forest Reserve. Structure and floristic composition of the plots at these floristically rich sites have been compared (Manokaran & Kochummen 1990); tree population dynamics in Sungei Menyala and Bukit Lagong from 1947 and 1949 respectively till 1959 summarised in Wyatt-Smith (1966) and till 1985, in Manokaran (1988); and from 1971 to 1984 in Pasoh in Manokaran (1988). Studies on tree population dynamics at Sungei Menyala and Bukit Lagong are probably the longest for primary rain forests.

In this paper we restrict ourselves to summarising information on various aspects of tree growth in these primary forests. In so doing, we attempt to provide answers to the following questions. How do populations of trees in a natural forest grow? How do the mean growth rates for species compare, especially for the various ecological groups? What are the rates of fast growth for individual trees, and what is the implication of this attribute to the forest regeneration process?

Site description and methods

Sungei Menyala Forest Reserve comprises 1244 *ha* of coastal lowland dipterocarp forest of the 'Red Meranti-Keruing' forest (Wyatt-Smith 1966) of the West Coast type (Wyatt-Smith 1987). Much of the reserve was selectively felled once around 1950 and today is considered as regenerated forest, within which lie three discrete patches of undisturbed primary forest totalling 19 *ha*. The study site is located in the largest (11.7 *ha*) of these three patches.

Bukit Lagong Forest Reserve is a hill dipterocarp forest covering 2529 *ha*. A major part of the forest was selectively felled: 755 *ha* between 1944 and 1945, and 1432 *ha* between 1952 and 1957. The study site lies within the remaining 160 *ha* of primary forest. The primary forest area contains both 'Seraya'-ridge and 'Balau kumus' types of forest (Wyatt-Smith 1966).

Pasoh Forest Reserve has been described as 'Red Meranti-Keruing' forest (Wyatt-Smith 1964) of the Central and Southern type (Wyatt-Smith 1987), and as 'Mixed Red Meranti' forest merging to 'Red Meranti' forest (Salleh 1968). The reserve consists of a core research area of about 650*ha* of primary lowland dipterocarp forest (location of the 2-*ha* plots) surrounded by a buffer zone of about 650*ha* of logged and regenerating forest and about 1000*ha* of primary hill dipterocarp forest. The regenerating buffer zone was selectively logged between 1955 and 1960.

Methods of plot establishment, tree enumeration and identification have already been described by Wyatt-Smith (1966) and Ashton (1971). In 200 × 100 *m* plots and subdivided 20 × 20 *m* subquadrats, all trees ≥ 10 *cm* DBH were identified and measured. The plots in Sungei Menyala and Bukit Lagong, established in 1947 and 1949 respectively, were recensused biennially till 1963 by Wyatt-Smith,

recensused after a 8-*y* gap in 1971 by Whitmore, and then recensused bienially from 1975 onwards by the authors. The plots in Pasoh, established in 1971, were recensused in 1979 and 1984 by the authors and Mohamad Ghazali Hj.Omar.

For purposes of other analyses not reported here, we classified all species enumerated into five species groups based on similar ecological characteristics. This was to overcome the problem of most species being represented by only a few individuals. Details of this classification, grouping species as emergents, main canopy, understorey, pioneer and late-seral species are provided in Manokaran and Kochummen (1987), and are based on a previous classification by Wyatt-Smith (1966).

The emergent, main canopy and understorey species are the climax (non-pioneer) species of Swaine and Whitmore (1988) and Whitmore (1989). The pioneer and late-seral species are equivalent to the short-lived, small-statured pioneers and long-lived, large-statured pioneers respectively of Swaine and Whitmore (1988) and Whitmore (1989), and we therefore use the latter terms in this paper.

Nomenclature for non-dipterocarps follows Whitmore (1972, 1973) and Ng (1978, 1989) and for dipterocarps Ashton (1982).

Results and discussion

Tree growth

Tree growth is generally measured as diameter or girth increments. Growth was slow in most of the trees enumerated, with 64% of trees growing at rates around 1 $mm\ y^{-1}$ (Figure 1). Slow growth in most of the trees in natural forest populations has also been shown previously for a dipterocarp forest in Sabah by Nicholson (1965). Low rates represent a major problem in the management of these forests for timber (Leslie 1977).

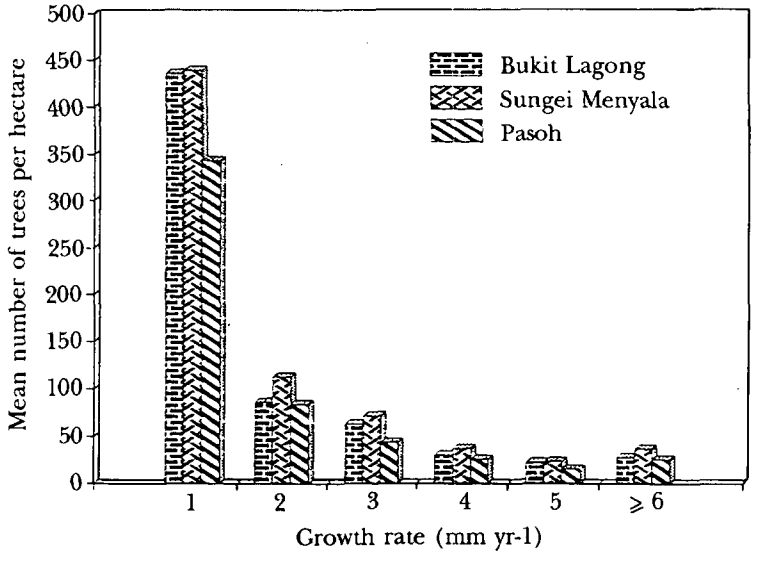

Figure 1. Frequencies of trees (≥ 10 *cm* DBH) in growth rate classes in primary dipterocarp forests

Table 1. Mean and maximum absolute growth rates for the 20 commonest species and the commonest secondary species at (a) the Bukit Lagong plot between 1949 - 85, (b) the Sungei Menyala plot between 1947-85. (Species are allocated to their ecological groups: E - emergent, MC - main canopy, U - understorey, SP - short-lived, small-statured pioneer, LP - long-lived, large-statured pioneer

(a) Bukit Lagong

Species	Number of trees	Mean years	Mean growth rate ($mm\ y^{-1}$)	Standard Deviation	Maximum rate ($mm\ y^{-1}$)	Initial DBH (cm)
Anisophyllea corneri (U) (Rhizophoraceae)	44	25.8	1.5	1.1	5.1	(10.3)
Barringtonia scortechnii (U) (Lecythidaceae)	22	32.0	0.5	0.4	2.1	(10.3)
Castanopsis schefferiana (MC) (Fagaceae)	15	24.9	3.0	2.0	6.9	(11.4)
Gluta elegans (MC) (Anacardiaceae)	19	34.3	0.5	0.4	1.5	(25.9)
Gonocaryum gracile (U) (Icacinaceae)	20	32.5	0.4	0.2	0.9	(17.1)
Hopea ferruginea (MC) (Dipterocarpaceae)	15	23.0	2.6	3.1	9.0	(10.5)
Hydnocarpus filipes (MC) (Flacourtiaceae)	108	27.0	0.9	0.5	2.2	(11.2)
Lindera oxyphylla (MC) (Lauraceae)	21	25.0	3.5	2.8	11.8	(11.2)
Macaranga triloba (SP) (Euphorbiaceae)	24	6.8	3.8	2.9	13.5	(12.2)
Neobalanocarpus heimii (E) (Dipterocarpaceae)	13	29.3	3.9	4.1	14.3	(76.4)
Payena lucida (U) (Sapotaceae)	13	33.6	1.6	1.7	4.9	(10.5)
Pellacalyx saccardianus (U) (Rhizophoraceae)	14	24.6	0.9	0.7	2.1	(19.8)
Pentace strychnoidea (MC) (Tiliaceae)	38	26.0	1.7	1.8	9.7	(14.9)
Scaphium macropodum (MC) (Sterculiaceae)	43	31.7	2.7	1.6	6.3	(42.7)
Schoutenia accrescens (MC) (Tiliaceae)	13	30.7	2.3	2.0	6.6	(40.7)
Shorea curtisii (E) (Dipterocarpaceae)	23	25.6	4.5	3.1	10.1	(64.3)
S. laevis (E) (Dipterocarpaceae)	33	31.5	2.7	2.3	9.3	(42.9)
Vatica lowii (MC) (Dipterocarpaceae)	23	25.4	1.7	1.0	3.6	(31.2)
Xanthophyllum maingayi (U) (Polygalaceae)	18	29.8	0.7	1.3	1.2	(17.1)
X. parvum (U) (Polygalaceae)	13	24.0	1.0	1.2	3.3	(17.9)
Macaranga gigantea (SP) (Euphorbiaceae)	3	4.2	4.0	3.8	7.8	(13.3)
M. hosei (SP) (Euphorbiaceae)	7	10.6	4.6	3.4	9.8	(11.0)
M. hypoleuca (SP) (Euphorbiaceae)	5	15.1	5.5	4.6	13.4	(11.5)
Endospermum malaccense (LP) (Euphorbiaceae)	12	23.0	2.1	1.8	5.5	(61.3)

(b) Sungei Menyala

Species	Number of trees	Mean years	Mean growth rate ($mm\ y^{-1}$)	Standard deviation	Maximum rate ($mm\ y^{-1}$)	Initial DBH (cm)
Alangium ebenaceum (U) (Alangiaceae)	20	23.3	1.2	1.1	4.5	(10.1)
Cyathocalyx pruniferus (MC) (Annonaceae)	19	14.1	2.3	1.5	5.6	(11.1)
Dipterocarpus verrucosus (E) (Dipterocarpaceae)	25	26.9	4.0	2.0	7.5	(60.4)
Durio griffithii (U) (Bombacaceae)	21	24.2	0.6	0.5	1.9	(10.4)
Fahrenheitia pendula (U) (Euphorbiaceae)	19	22.0	1.5	1.3	5.6	(10.5)
Gironniera nervosa (U) (Ulmaeae)	24	17.8	2.0	2.1	6.9	(10.0)
Hydnocarpus filipes (MC) (Flacourtiaceae)	17	23.3	1.2	0.7	2.0	(15.3)
Ixonanthes icosandra (MC) (Linaceae)	20	21.0	2.6	1.3	5.8	(22.0)
Neoscortechinia kingii (U) (Euphorbiaceae)	17	22.8	0.9	0.8	2.6	(20.9)
Ochanostachys amentacea (MC) (Olacaceae)	26	27.7	1.3	1.0	3.9	(11.6)
Payena lucida (U) (Sapotaceae)	18	25.1	1.8	0.9	3.4	(12.3)
Pimelodendron griffithianum (U) (Euphorbiaceae)	19	23.9	1.8	1.1	4.3	(12.9)
Porterandia anisophylla (U) (Rubiaceae)	38	22.0	1.6	1.5	5.1	(11.0)
Santiria laevigata (MC) (Burseraceae)	47	27.1	2.0	1.5	6.1	(26.8)
S. tomentosa (MC) (Burseraceae)	21	27.7	1.9	1.7	5.0	(20.2)
Shorea macroptera (E) (Dipterocarpaceae)	32	25.7	4.2	2.3	8.1	(15.1)
S. parvifolia (E) (Dipterocarpaceae)	27	23.1	3.2	3.2	14.6	(11.6)
S. pauciflora (E) (Dipterocarpaceae)	19	30.3	3.8	2.5	9.6	(38.3)
Trigoniastrum hypoleucum (MC) (Trigoniaceae)	27	20.9	1.8	1.5	6.9	(11.3)
Xerospermum noronhianum (U) (Sapindaceae)	22	20.2	1.5	1.1	4.0	(12.5)
Macaranga gigantea (SP) (Euphorbiaceae)	2	9.1	4.5	3.2	6.6	(11.1)
M. conifera (LP) (Euphorbiaceae)	6	20.3	2.8	2.0	6.4	(36.4)
Endospermum malaccense (LP) (Euphorbiaceae)	5	30.7	4.2	2.3	6.8	(32.4)
Artocarpus elasticus (LP) (Moraceae)	5	30.7	1.5	1.2	3.2	(38.2)

Mean and maximum growth rates

For the longer-term plots at Bukit Lagong and Sungei Menyala, the mean and maximum absolute growth rates for the 20 commonest species, and for the commoner short-lived, small pioneer and long-lived, large pioneer species, are given in Table 1. The calculated mean rates include all size classes during the period of study. We examined the common species because they provided us with a sufficient sample size each.

Mean DBH increment for understorey species ranged from 0.4 to 1.6 *mm* y^{-1} at the Bukit Lagong plot and from 0.6 to 2.0 *mm* y^{-1} at the Sungei Menyala plot (Table 1). The ranges for the other species groups at Bukit Lagong and Sungei Menyala were respectively 0.5 to 3.5 *mm* and 1.2 to 2.6 *mm* y^{-1} for main canopy species, 2.7 to 4.5 *mm* and 3.2 to 4.2 *mm* y^{-1} for emergent species, and 2.1 to 5.5 *mm* and 1.5 to 4.5 *mm* y^{-1} for both classes of pioneer species. Species groups therefore differed in their rates of growth in the following sequence: understorey < main canopy < emergent ≈ pioneers. Rates of growth of shade-tolerant understorey species have previously been shown to be lower than those of species of other groups (see Lieberman & Lieberman 1987, Manokaran & Kochummen 1987).

Maximum growth rates by individual trees were achieved by either short-lived, small pioneers or dipterocarps. At Bukit Lagong, the highest rates were 14.3, 13.5 and 13.4 *mm* y^{-1} for *Neobalanocarpus heimii, Macaranga triloba* and *M. hypoleuca* respectively. At Sungei Menyala, they were 14.6, 9.6 and 8.1 *mm* y^{-1} for *Shorea parvifolia, S. pauciflora* and *S. macroptera* respectively. Thus, while short-lived, small pioneers grow rapidly in large gaps and clearings in the primary forests, rates of growth of some emergent species are comparable to those of these pioneers (see also Manokaran & Kochummen 1987). Data from plantations and the arboretum at the Forest Research Institute Malaysia indicate that individual trees of several of the common dipterocarp species may grow at rates of 8.0 to 16.0 *mm* DBH per year in their early years (Ng & Tang 1974, Wyatt-Smith 1987). *S. parvifolia* and *S. macroptera*, together with another emergent dipterocarp species, *S. leprosula*, are known to be vigorous, aggressive species common in young, regenerated forest (Wyatt-Smith 1954, 1963b, Cousens 1965).

Fast growth in trees

While the majority of individuals in a population of trees grow slowly (see Figure 1), some individuals show high growth rates. Table 2 lists trees that showed rapid growth (> 5 *mm* y^{-1}) from small size (< 20 *cm* DBH) over a long period (present for > 10 enumerations) for the Bukit Lagong and Sungei Menyala plots. The species in the lists have been classified as light hardwoods (LHW), medium hardwoods (MHW) and heavy hardwoods (HHW), the groupings being based on the density of timbers according to the Malayan Grading Rules (Anonymous 1968).

A total of 16 trees at the Bukit Lagong plot with initial low diameter, and 21 at the Sungei Menyala plot, showed fast growth over a long period (maximum of 36 and 38 years respectively). They were all still alive at the census in 1985, and

Table 2. Trees with low initial diameter (< 20 *cm* DBH) and fast growth rate (> 5 *mm* y^{-1}) over a long period at the (a) Bukit Lagong plot, (b) Sungei Menyala plot.(Species are allocated to their ecological groups: E - emergent, MC - main canopy, U - understorey; species are also classified according to timber density: LHW - light hardwood, MHW - medium hardwood, HHW - heavy hardwood. An '*' means tree not present at initial census)

(a) Bukit Lagong

Species	Wood density class	Growth rate (*mm* y^{-1})	Initial diameter (*cm*)	Last diameter (*cm*)
Hopea ferruginea (MC) (Dipterocarpaceae)	LHW	5.7	10.7*	27.2
H. ferruginea (MC) (Dipterocarpaceae)	LHW	9.0	10.5*	36.1
Neobalanocarpus heimii (E) (Dipterocarpaceae)	HHW	5.4	17.9	37.3
Shorea curtisii (E) (Dipterocarpaceae)	LHW	5.6	12.2	34.2
Elaeocarpus jackianus (U) (Elaeocarpaceae)	LHW	7.7	11.0	38.0
E. floribundus (MC) (Elaeocarpaceae)	LHW	8.3	11.5	40.2
Castanopsis schefferiana (MC) (Fagaceae)	LHW	6.2	17.1	40.0
Calophyllum tetrapterum (MC) (Guttiferae)	LHW	8.3	12.5	41.8
Lindera oxyphylla (MC) (Lauraceae)	LHW	12.3	11.2*	51.5
Litsea castanea (MC) (Lauraceae)	LHW	7.7	13.8*	37.8
Adenanthera pavonina (MC) (Leguminosae)	MHW	6.3	15.8	38.7
Dialium laurinum (MC) (Leguminosae)	HHW	7.1	18.9	44.0
Archidendron bubalinum (U) (Leguminosae)	?	5.1	11.3*	26.9
Ficus lamponga (MC) (Moraceae)	LHW	7.9	10.6*	31.3
Pentace strychnoidea (MC) (Tiliaceae)	LHW	5.1	16.7	35.0
Schoutenia accrescens (MC) (Tiliaceae)	LHW	5.3	16.5	35.1

(b) Sungei Menyala

Species	Wood density class	Growth rate ($mm\ y^{-1}$)	Initial diameter (cm)	Last diameter (cm)
Monocarpia marginalis (MC) (Annonaceae)	LHW	5.5	11.4	30.2
Santiria laevigata (MC) (Burseraceae)	LHW	5.7	19.6	40.2
S. laevigata (MC) (Burseraceae)	LHW	5.4	19.2	38.2
S. laevigata (MC) (Burseraceae)	LHW	5.8	19.5	40.2
Dipterocarpus verrucosus (E) (Dipterocarpaceae)	MHW	5.9	19.0	40.5
Shorea dasyphylla (E) (Dipterocarpaceae)	LHW	7.0	11.4*	36.1
S. hopeifolia (E) (Dipterocarpaceae)	LHW	5.3	19.0	38.5
S. macroptera (E) (Dipterocarpaceae)	LHW	7.7	18.4	47.4
S. macroptera (E) (Dipterocarpaceae)	LHW	7.5	10.2*	34.7
S. macroptera (E) (Dipterocarpaceae)	LHW	5.6	17.7	39.4
S. macroptera (E) (Dipterocarpaceae)	LHW	8.1	15.1	46.8
S. macroptera (E) (Dipterocarpaceae)	LHW	5.1	19.6	37.7
S. macroptera (E) (Dipterocarpaceae)	LHW	6.1	14.3	36.5
S. macroptera (E) (Dipterocarpaceae)	LHW	6.4	13.3	37.9
S. parvifolia (E) (Dipterocarpaceae)	LHW	5.2	17.3	39.7
Castanopsis inermis (MC) (Fagaceae)	MHW	5.1	13.2	30.9
Garcinia parvifolia (MC) (Guttiferae)	MHW	7.6	10.6*	32.2
Litsea machilifolia (MC) (Lauraceae)	LHW	6.3	17.7	41.3
L. maingayi (MC) (Lauraceae)	LHW	5.9	19.7	42.5
L. maingayi (MC) (Lauraceae)	LHW	6.2	11.2*	30.0
Artocarpus lanceifolius (MC) (Moraceae)	MHW	5.3	11.6	33.5

72% of them were present at the initial census at plot establishment in 1947 or 1949. Canopy species (emergent and main canopy) formed 95% of the total of 37 trees, the remaining being understorey species. The fast-growing short-lived, small pioneer species are absent from the lists as none survived long enough. The shade-tolerant understorey species are generally slow-growing but as shown by the results, individual trees may show relatively fast growth. This has also been reported by Nicholson (1965). Light hardwoods formed 80% of these 37 fast-growing trees. Heavy hardwood species, with dense, hard timber, have been noted

to respond to increased light more slowly, and to show less increase in growth than light hardwood species (Wyatt-Smith 1963a, 1963b), but as shown in the table, individual trees can grow fast. Almost half the 37 fast-growing trees are dipterocarps and they are the majority of the fast growers at the Sungei Menyala plot.

The fastest-growing individual at the Bukit Lagong plot, a tree of *Lindera oxyphylla* with a DBH increment of 12.3 $mm\ y^{-1}$, reached a diameter greater than 50 *cm* in 34 years. At the Sungei Menyala plot, a tree of *Shorea macroptera* with the highest long-term DBH increment of 8.1 $mm\ y^{-1}$, reached a diameter of just under 50 *cm* in 38 years.

For the relatively shorter-term Pasoh site, with sample size four times that of the plots in Sungei Menyala and Bukit Lagong, the maximum growth rates achieved by individual trees are shown in Table 3. This is for trees of initial diameter of 20 *cm* and less and with growth rates of 7 $mm\ y^{-1}$ and greater, over periods of 8 or 13 years. A total of 29 trees with initial low diameter showed fast growth, with 20 of these trees present throughout the period of 13 years from the first census in 1971 to the last census in 1984. If fast growth is defined to be a lower value of 5 $mm\ y^{-1}$ and greater, then a total of 62 trees with initial low diameter showed fast growth. Of these, not shown in the table, 43 trees were present throughout the 13-*y* period.

Canopy species (emergent and main canopy) formed 79% of the 29 trees, the remaining being understorey species. Of the 62 trees, 77% were canopy species and the remaining, understorey species. Thus, as also shown in the Bukit Lagong and Sungei Menyala plots, individual trees of shade-tolerant understorey species are capable of relatively fast growth.

Light hardwoods formed 45% of the 29 fast-growing trees with medium hardwoods forming another 35%. There was only one tree of heavy hardwood species with fast growth - a tree of *Shorea maxwelliana* (Dipterocarpaceae) with a growth rate of 9.5 $mm\ y^{-1}$, this being one of the faster growth rates seen. This is an exception to the notion that heavy hardwood species are slow growers.

Just over a quarter of the 29 fast-growing trees are dipterocarps. These are generally the faster-growing individuals, with rates of 8.5 $mm\ y^{-1}$ and greater. With such growth rates, they are likely to reach larger size in a fairly short period, as exemplified by an individual of *Shorea macroptera* at the Sungei Menyala plot.

Growth of short-lived pioneers

Growth rates of some short-lived, small pioneers and long-lived, large pioneers have been provided in Table 1. Short-lived pioneers, of necessity, need to grow fast as they die in shade.

In the Bukit Lagong plot, two trees of *Macaranga triloba* (the first of 12 recruits) were recruited to 10 *cm* DBH, 25 years after gap formation at the south-eastern corner. This is an indication of the time span for growth to that size from seed germination.

Table 3. Individual trees with low initial diameter (< 20 *cm* dbh) and fast growth rate (>7 *mm* y^{-1}) in the plots at Pasoh Forest Reserve. (Species are allocated to their ecological groups: E - emergent, MC - main canopy, U - understorey. Species are also classified according to timber density: LHW - light hardwood, MHW - medium hardwood, HHW - heavy hardwood)

Species	Wood density class	Growth rate (*mm* y^{-1})	Initial diameter (*cm*)	Last diameter (*cm*)	Growth period (y)
Buchanania sessifolia (U) (Anacardiaceae)	MHW	8.6	10.6	14.9	5
Pentaspadon motleyi (MC) (Anacardiaceae)	LHW	8.0	12.7	23.0	13
Monocarpia marginalis (MC) (Annonaceae)	LHW	8.2	15.8	19.9	5
Monocarpia marginalis (MC) (Annonaceae)	LHW	7.6	14.0	23.9	13
Xylopia ferruginea (MC) (Annonaceae)	LHW	9.5	18.5	30.6	13
Shorea lepidota (E) (Dipterocarpaceae)	LHW	8.8	14.5	18.9	5
Shorea leprosula (E) (Dipterocarpaceae)	LHW	8.5	14.0	25.1	13
Shorea maxwelliana (E) (Dipterocarpaceae)	HHW	9.5	10.8	22.8	13
Shorea parvifolia (E) (Dipterocarpaceae)	LHW	9.0	16.2	28.0	13
Shorea parvifolia (E) (Dipterocarpaceae)	LHW	9.8	10.5	15.4	5
Shorea parvifolia (E) (Dipterocarpaceae)	LHW	8.7	17.5	28.6	13
Elaeocarpus palembanicus (U) (Elaeocarpaceae)	?	9.0	15.9	20.4	5
Aporusa bracteosa (U) (Euphorbiaceae)	?	7.5	18.1	28.4	13
Cleistanthus sumatranus (U) (Euphorbiaceae)	?	8.2	10.2	20.5	13
Sapium baccatum (MC) (Euphorbiaceae)	LHW	8.0	16.9	27.2	13
Castanopsis megacarpa (MC) (Fagaceae)	MHW	8.1	11.1	21.6	13
Castanopsis megacarpa (MC) (Fagaceae)	MHW	8.1	18.8	29.1	13
Castanopsis rhamnifolia (MC) (Fagaceae)	MHW	8.1	16.2	22.7	8
Castanopsis schefferiana (MC) (Fagaceae)	MHW	8.6	17.5	28.8	13
Castanopsis schefferiana (MC) (Fagaceae)	MHW	7.9	13.1	23.2	13
Lithocarpus rassa (MC) (Fagaceae)	MHW	7.2	11.3	14.9	5
Lithocarpus wallichianus (MC) (Fagaceae)	MHW	9.7	12.1	24.7	13
Quercus argentata (E) (Fagaceae)	MHW	7.5	14.0	23.8	13
Endiandra maingayi (MC) (Lauraceae)	?	8.1	18.5	28.9	13

Continued

Table 3 (continued)

Archidendron bubalinum (U) (Leguminosae)	LHW	7.7	18.1	24.3	8
Millettia atropurpurea (MC) (Leguminosae)	MHW	7.7	18.5	28.0	13
Aglaia maingayi (U) (Meliaceae)	?	7.6	10.2	14.0	5
Horsfieldia superba (MC) (Myristicaceae)	LHW	7.3	18.5	27.7	13
Sarcotheca griffithii (MC) (Oxalidaceae)	LHW	7.2	16.2	25.4	13

Growth of short-lived pioneers in artificially created gaps, where there is greater crown exposure, and possibly less root competition, may even be faster. For example, we found that the largest of eight trees of *Macaranga hypoleuca* and four trees of *M. gigantea* in a 20 × 50 *m* area in Pasoh Forest Reserve, had grown to diameters of 15.4 and 11.7 *cm* respectively by August 1988, 17 years after destructive sampling had been carried out by Kato *et al.* (1978) to estimate plant biomass for the forest. In another 20 × 100 *m* area in the same forest, treated similarly two years later by Kato *et al.* (1978) as well, the largest of seven trees of *M. hosei* and three trees of *M. hypoleuca* had grown to diameters of 16.3 and 10.3 *cm* respectively in 15 years by August 1988. Such growth in these instances was from seed germination.

The highest growth rates by short-lived pioneers are likely to be shown in areas with the greatest crown exposure. *Macaranga gigantea* was recorded to reach a maximum diameter of 38 *cm* in a sample of 160 trees, 15 years old, at Sungei Kroh, Peninsular Malaysia (Kochummen 1966). In 1945, this forest reserve had been clear-felled except for the larger trees, burnt prior to rice cultivation, and then abandoned in late 1946. *Ochroma lagopus* attained 35 *cm* DBH in only five years in an abandoned pasture at La Selva, Costa Rica (Hartshorn 1978), but whether this was from already established saplings or from seed is not clear. Thirty-seven trees of *Harungana madagascariensis* (26 trees) and *Trema orientalis* (11 trees) exceeded 10 *m* in height five years after 2 *ha* of forest were cleared at Atewa Range Forest Reserve in Ghana (Swaine & Hall 1983).

Time taken to grow to canopy level

There may be variations in the diameter at which individual trees of canopy species reach the canopy in the primary forest. Poore (1968) estimated that trees at the Jengka Forest Reserve had generally reached the canopy at a diameter of 29 *cm* at breast height. We consider 30 *cm* DBH to be the approximate size at which canopy species reach the canopy. Based on this consideration, and reflecting on data from Table 2, fast-growing trees of canopy species at the Bukit Lagong plot took 18 to 34 years, with an average of 25.2 years, to reach the canopy from a diameter below 20 *cm*, and 18 to 34 years also, with an average of 25.0 years, for trees below 15 *cm* diameter. At the Sungei Menyala plot, the corresponding

figures were 16 to 38 years, with an average of 27.7 years for trees below 20 *cm* diameter, and 26 to 38 years, with an average of 30.9 years for trees below 15 *cm* diameter.

In a previous section, a cohort of a short-lived pioneer species at Bukit Lagong was estimated to reach a DBH of 10 *cm* in about 25 years from seed germination. This size was reached by uninterrupted fast growth in a large gap.

There is no information as to how long primary forest species take to reach a DBH of 10 *cm* from seed germination, except in plantations and arboreta. Whitmore (1984) notes that under very good conditions, germination is followed by an initial slow phase as a seedling and then by a phase of accelerating growth which is approximately linear for some time. Manokaran (1988) has shown strong auto correlation in growth, indicating that trees tend to increase linearly in diameter over long periods. The fastest-growing non-pioneer species have been shown to have similar growth rates as short-lived pioneer species (see Table 1), but unlike primary forest species, short-lived pioneers show uninterrupted fast growth even as seedlings. Based on these considerations, therefore, fast-growing canopy species in the primary forest, especially dipterocarps, may take about 30 years from seed germination to reach a size of 10 *cm* DBH, and then a further 30 to 35 years to reach the canopy. Trees of 30 *cm* DBH (*ca.* 1 *m* girth) may be as young as 60 years.

Conclusions

As shown by this study, most trees in natural dipterocarp forest populations grow very slowly. Within such populations, shade-tolerant understorey species grow at much slower rates than other species. Light-demanding short-lived and long-lived pioneers, as well as emergent species, grow more rapidly. Short-lived pioneers, of necessity, need to grow fast as they die in shade, while emergent species, in the fight for survival, require to grow fast to reach the canopy level.

The study clearly showed that some individual trees in the natural dipterocarp forest populations can grow at relatively high rates. Most of these are of canopy species (emergent and main canopy), mainly light hardwoods, and up to half, dipterocarp species. While understorey species are shade tolerant and slow growing, and heavy hardwoods respond to increased light more slowly than light hardwoods, certain individuals of these groups of species are capable of relatively fast growth as well.

Individuals of canopy species growing at relatively fast rates, especially dipterocarps, are likely to reach larger size in a fairly short time. Direct and indirect evidences suggest that these individuals in the primary forest may take about 60 years from seed germination to reach a size of 30 *cm* DBH at which their crowns would be at the canopy.

Acknowledgements

The plots at Bukit Lagong and Sungei Menyala were established by J. Wyatt-Smith and those at Pasoh by P. S. Ashton. Trees and herbarium specimens were identified by J. Wyatt-Smith and T. C. Whitmore (Bukit Lagong and Sungei Menyala), P. S. Ashton (Pasoh), and by the second author (all sites). Field staff of the Forest Research Institute Malaysia assisted in carrying out enumerations, computing assistance was provided by P. F. Chong, and M. D. Swaine advised. Dasima Ramudin typed the manuscript of this paper.

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