SHORT-TERM POPULATION DYNAMICS OF DIPTEROCARP TREES IN A LOWLAND RAIN FOREST IN PENINSULAR MALAYSIA

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Received November 1992

MANOKARAN, N., ABD. RAHMAN KASSIM, AZMAN HASSAN, QUAH, E. S. & CHONG, P. F. 1992. Short-term population dynamics of dipterocarp trees in a lowland rain forest in Peninsular Malaysia. Based on an initial census in 1987 and a repeat census in 1990 of all trees ≤ 1 *cm* DBH in a 50-*ha* plot in Pasoh Forest Reserve, the Dipterocarpaceae suffered a significantly higher mortality of 6.88% than the total flora which suffered a mortality of 3.81%. With about 80% of the total stems in the 1 to ≤ 5 *cm* DBH class for both the Dipterocarpaceae and the plot flora, mortality at this size class was significantly higher than in the ≥ 5 *cm* size class for both groups. Recruitment of 4.80% into the lowest size class for the Dipterocarpaceae was significantly higher than that at 1.55% for the plot flora. Resultant population change for both groups was similar, a reduction of 2.26% for the plot and 2.08% for the Dipterocarpaceae. At the species level, three categories of dynamic changes were recognised. The commonest light hardwood *Shorea* species, and one each of *Hopea* and *Parashorea*, suffered high mortality compensated by high recruitment. *Shorea leprosula* was the most dynamic species. In the medium hardwood species of *Dipterocarpus*, and the heavy hardwood species of *Vatica* and in *Neobalanocarpus heimii*, both mortality and recruitment were low. In the balau heavy hardwood group of *Shorea* species, mortality was low but recruitment was moderately higher.

Key words: Rain forest - dipterocarps - mortality - recruitment - population change

MANOKARAN, N., ABD. RAHMAN KASSIM, AZMAN HASSAN, QUAH, E.S. & CHONG, P.F. 1992. Dinamik jangka pendek populasi kaum dipterokap di sebuah hutan hujan pamah Semenanjung Malaysia. Berasaskan pada bancian pertama pada 1987 dan bancian semula dalam tahun 1990 terhadap semua pohon ≤ 1 sm perepang paras dada (ppd) di petak percubaan seluas 50 hektar di hutan simpan Pasoh, kematian kaum Dipterocarpaceae berjumlah 6.88% adalah lebih tinggi bererti dibandingkan dengan keseluruhan flora iaitu 3.81% sahaja. Hampir 80% daripada kesemua pohon daripada famili Dipterocarpaceae dan juga bukan Dipterocarpaceae terkandung dalam kelas ppd 1 - ≤ 5 sm, kematian di dalam kelas saiz ini adalah lebih tinggi bererti jika dibandingkan dengan kelas saiz ≥ 5 sm bagi kedua-dua kumpulan tersebut. Penokokan yang berjumlah 4.80% kedalam saiz terkecil Famili Dipterocarpaceae adalah lebih tinggi bererti berbanding dengan 1.55% untuk keseluruhan flora petak tersebut. Hasilan perubahan populasi untuk kedua-dua kumpulan adalah serupa, pengurangan sebanyak 2.26% untuk petak dan 2.08% untuk Dipterocarpaceae. Di peringkat spesies pula, tiga kategori perubahan dinamik telah dapat dikenal pasti. Kayu keras ringan spesies *Shorea* yang paling biasa dan satu dari *Hopea* dan juga *Parashorea* mengalami kamortalan tinggi, tetapi menerima pampasan penokokan yang tinggi juga. *Shorea leprosula* merupakan spesies yang paling dinamik. Di dalam kayu keras sederhana spesies *Dipterocarpus* dan kayu keras berat spesies-spesies *Vatica* dan juga *Neobalanocarpus heimii*, kemortalan dan penokokan adalah rendah. Dalam kumpulan kayu keras berat balau dari spesies-spesies *Shorea*, kemortalan didapati rendah tetapi penokokan didapati lebih sederhana tinggi.

Introduction

Between 1985 and 1988, the Forest Research Institute Malaysia (FRIM) established a 50-*ha* plot at Pasoh Forest Reserve, Negeri Sembilan, to monitor long- term changes in a primary forest. All woody plants of 1 *cm* diameter at breast height (DBH) and greater were censused and the floristic composition of the trees and shrubs in the plot summarised in Kochummen *et al.* (1990). Additionally, the stand structure of the trees and shrubs in the plot was summarised by Manokaran and LaFrankie (1990), the structure and composition of the family Dipterocarpaceae summarised by Manokaran *et al.* (1991), an account of fruit trees in the plot given in Saw *et al.* (1991), and the flora of the plot compared with that of the Malay Peninsula in Kochummen *et al.* (1992). The stand table and distribution of all species in the plot are also provided in Manokaran *et al.* (1992). The plot was recensused in 1990.

The recensus has allowed us to examine short-term dynamics of tree populations in the plot. Relatively few studies on population dynamics have been carried out in tropical rain forests, and these have been reviewed in Swaine *et al.* (1987). In Peninsular Malaysia, long-term studies on tree population dynamics in hill and lowland dipterocarp forests have been carried out for trees of 10 *cm* DBH and greater by Wyatt-Smith (1966), Manokaran and Kochummen (1987) and Manokaran (1988). In the present study, we are able to examine, for the first time, population dynamics to a diameter as low as one centimetre.

In this paper, we restrict our analyses to the family Dipterocarpaceae, the main timber family of the Southeast Asian region. In Peninsular Malaysia members of this family occur up to an altitude of about 1200 *m* above sea level, covering the main forest types of lowland dipterocarp forest, hill dipterocarp forest and the upper dipterocarp forest, with a poorer representation of species in the upper zone (Symington 1943). They are also represented in edaphic climax formations such as peat swamp forests, riparian fringes and heath forests. Where they occur, dipterocarp species generally form a high proportion of the emergent and main canopy strata of the forest. In this 50-*ha* plot the frequency of dipterocarps is just over 9% of the total stems, and basal area accounts for 24% of the total (Manokaran *et al.* 1991).

In Pasoh, species of Dipterocarpaceae include a very good representation of the red meranti group of the genus *Shorea*. Balau (heavy hardwood species of the genus *Shorea*), keruing (*Dipterocarpus* spp.), as well as *Hopea* and *Vatica* are also fairly well represented. Chengal, *Neobalanocarpus heimii*, is the second most common dipterocarp.

Of the 30 dipterocarp species in the plot, 18 are light, 5 medium and 7 heavy hardwoods. This is a classification of timbers of Peninsular Malaysia based on density (Anonymous 1968).

In examining population dynamics, we looked for answers to the following questions. How do mortality and recruitment rates for the family Dipterocarpaceae compare with those of the whole plot? How do individual species of the family differ in these attributes? Is mortality at the sapling stage significantly higher than that at larger sizes? In a following paper we will be examining population dynamics of the total plot flora to answer similar and other questions.

Site description and methods

Pasoh Forest Reserve is an inland forest, 2° 59' N and 102° 19' E, at about 140 *km* southeast of Kuala Lumpur, amidst a broad expanse of flat lands and gently rolling ridges that abut the westward side of the Main Range. The vegetation is primary rain forest and falls within the south-central subtype of the 'Red Meranti-Keruing' forest sub-type of Wyatt-Smith (1987). The upper canopy is dominated by red meranti, *Shorea* section Muticae, especially *S. leprosula, S. acuminata* and *S. macroptera.* Other important canopy emergents are keruing (*Dipterocarpus cornutus),* balau (*Shorea maxwelliana*) and chengal (*Neobalanocarpus heimii*).

Mean annual rainfall at Pasoh is about 2000 *mm,* which is among the driest stations in Peninsular Malaysia. Further details of the ecology and vegetation of Pasoh Forest Reserve are provided in Kochummen *et al.* (1990) and Soepadmo and Kira (1977).

The plot is a 50-*ha* rectangle 1 *km* long and 0.5 *km* wide. The enumeration included all free standing trees and shrubs of one centimetre diameter and greater. Climbers were excluded. The details by which the plot was surveyed, the trees measured and species identified are recounted in Manokaran *et al.* (1990).

Tree counts and diameter measurements at the initial census began in February 1986 and ended in March 1988. For this paper the initial census is dated as 1987. The recensus began in January 1990 and ended in October of the same year.

Results

Mortality

Mortality of 6.88% for the family Dipterocarpaceae was significantly higher (X^2=683.0, P<0.001) than that of 3.81% for the whole plot (Table 1).

Of the 30 dipterocarp species, 21 had an initial population of more than 100 individuals which we consider a reasonable population size for studies on dynamics. Five of these, *Shorea leprosula, S. parvifolia, S. lepidota* , *S. acuminata* and *S. ovalis,* all light hardwoods, suffered significantly higher mortalities than the family rate of 6.90% for the 21 species (Table 1). Another six species, all light hardwoods, had mortality rates which were not significantly different from that of the family rate. The remaining ten species suffered significantly lower mortalities than the family as a whole. These included six heavy hardwoods, including the two commonest dipterocarps, *S. maxwelliana* and *Neobalanocarpus heimii,* and only one light hardwood, *S. pauciflora.*

Three species, *Shorea leprosula, S. parvifolia* and *S. lepidota,* had high mortality rates of greater than 10%. We consider a 10% mortality to be high in view of the short time lapse between the two censuses. *S. leprosula* and *S. parvifolia* are among the commonest dipterocarps in the plot.

Mean annual rainfall at the nearest climatological station at Kuala Pilah, about 37 *km* away, is 1850 *mm*, and is distributed fairly evenly throughout the year. During 1986 to 1990, when there was no continuous record of rainfall at Pasoh, rainfall at this station varied from a low of 1125 *mm* in 1986 to a high of 1690 *mm* in 1990. Although these values are lower than the mean annual value, there was no unusual prolonged period of dryness during this 5-*y* period (Figure 1) which could have induced an unusually high level of mortality in the majority of the woody flora in the 50-*ha* plot. The low rainfall for February 1989 appears to be an aberration, hedged in by two months of heavy rainfall. Faulty rainfall recording is suspected.

The overall results are indicative of greater stability in populations of medium and heavy hardwood species of the dipterocarps than in the light hardwoods. The species of *Dipterocarpus* in particular appear to be a rather stable group.

Table 1. Tree mortality in species of dipterocarp (mortality in species with more than 100 individuals each is compared with that of the family)

Species	Timber density class	Frequency in 1987	Number remaining in 1990	Mortality (%)	X^2	P
Anisoptera costata	L	22	22	0.00	-	-
Anisoptera laevis	L	137	132	3.65	2.26	>0.1
Anisoptera megistocarpa	L	53	50	5.66	-	-
Dipterocarpus cornutus	M	1475	1436	2.64	41.64	<0.001
Dipterocarpus costulatus	M	626	613	2.08	22.70	<0.001
Dipterocarpus crinitus	M	236	229	2.97	5.69	<0.05
Dipterocarpus kunstleri	M	75	73	2.67	-	-
Dipterocarpus sublamellatus	M	4	4	0.00	-	-
Hopea dryobalanoides	L	696	649	6.75	0.02	>0.5
Hopea mengerawan	L	451	426	5.54	1.30	>0.25
Hopea sangal	L	18	18	0.00	-	-
Neobalanocarpus heimii	H	3291	3180	3.37	63.84	<0.001
Parashorea densiflora	L	158	150	5.06	0.83	>0.25
Shorea acuminata	L	2211	2014	8.91	13.84	<0.001
Shorea bracteolata	L	1135	1047	7.75	1.27	>0.25
Shorea dasyphylla	L	43	40	6.98	-	-
Shorea guiso	H	720	694	3.61	12.15	<0.001
Shorea hopeifolia	L	60	57	5.00	-	-
Shorea lepidota	L	1172	1045	10.84	28.20	<0.001
Shorea leprosula	L	3017	2505	16.97	475.68	<0.001
Shorea macroptera	L	1597	1489	6.76	0.05	>0.75
Shorea maxwelliana	H	5682	5433	4.38	56.21	<0.001
Shorea multiflora	L	3	3	0.00	-	-
Shorea ochrophloia	H	442	424	4.07	5.51	<0.05
Shorea ovalis	L	1308	1193	8.79	7.26	<0.01
Shorea parvifolia	L	1685	1455	13.65	119.31	<0.001
Shorea pauciflora	L	2370	2241	5.44	7.87	<0.01
Vatica bella	H	1669	1629	2.40	52.75	<0.001
Vatica maingayi	H	92	86	6.52	-	-
Vatica pauciflora	H	470	455	3.19	10.08	<0.01
Dipterocarpaceae						
All species	-	30918	28792	6.88	-	-
21 commonest species	-	30548	28439	6.90	-	-
Whole plot	-	335240	322474	3.81	-	-

Note: L = light hardwood, M = medium hardwood, H = heavy hardwood

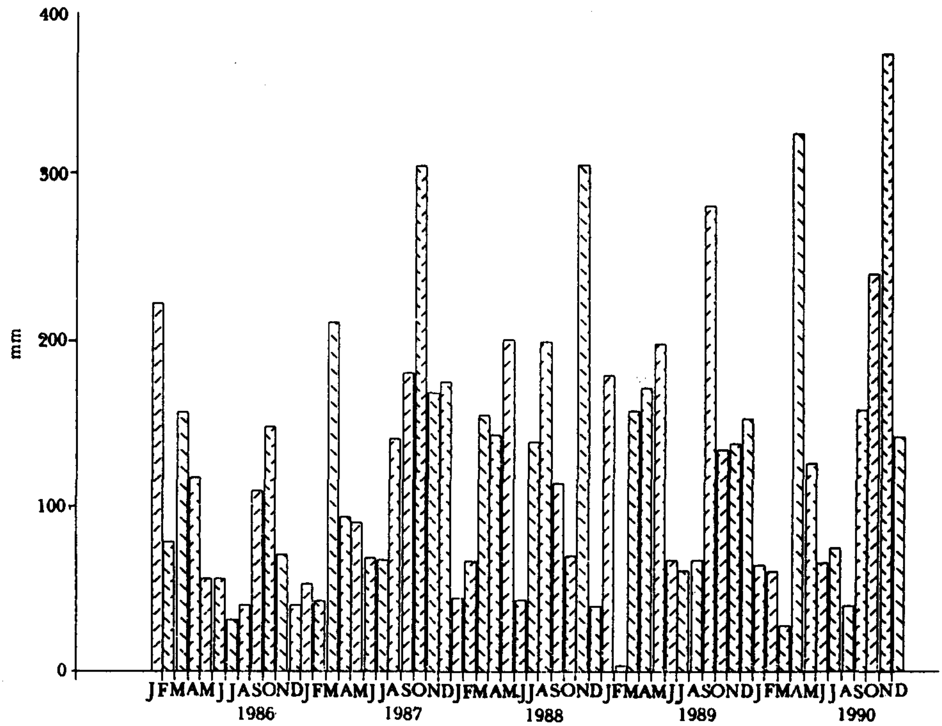

Figure 1. Monthly rainfall at the climatological station at Kuala Pilah for the period 1986 -1990

Mortality in size classes

We separated mortality into two size classes, one below 5*cm* diameter at breast height (DBH)where we expect a relatively higher turnover, and one of 5 *cm* DBH and greater.

Mortality of stems in the 1 to < 5 *cm* DBH class for the dipterocarps was 7.63%, significantly higher (X^2=754.6, P< 0.001) than the comparable rate of 3.93% for the plot itself (Table 2a). For stems ≥ 5 *cm* DBH, the mortality rate of 4.08% for the dipterocarps was significantly higher (X^2=9.92, P < 0.01) than the rate of 3.34% for the plot.

For the woody flora of the whole plot, which consists of a mix of stature classes such as 'shrub', 'treelet', 'understorey', 'canopy' and 'emergent' (see Kochummen *et al.* 1990 for the basis of stature class assignment), mortality in the 1 to < 5 *cm* DBH class of 3.93% was significantly higher (X^2=50.67, P< 0.001) than the mortality of 3.34% in the ≥ 5 *cm* DBH class. For the dipterocarps, mortality of 7.63% at the 1 to < 5 *cm* DBH class was significantly higher (X^2=102.2, P< 0.001) than the mortality of 4.08% at the ≥ 5 *cm* DBH class. Thus, mortality for the whole woody flora and for the dipterocarps occurred mainly in lower size class, but turnover for the dipterocarps was much more rapid. At the ≥ 10 *cm* DBH class, mortality of 3.61% for the dipterocarps was not significantly different (X^2=0.01, P > 0.9) from the rate of 3.57% for the whole woody flora. However, over the longer term of 13 years in 8 *ha* in the same forest, Manokaran (1988) found that

Table 2a. Tree mortality in species of dipterocarp in two size classes. Mortality in species with more than 100 individuals each at the respective size class, is compared with the respective rates for the family

Species	Timber density class	Frequency in 1987 1 - <5 *cm* DBH	Number remaining in 1990 1- <5 *cm* DBH	Mortality (%)	X^2	P	Frequency in 1987 ≥ 5 *cm* DBH	Number remaining in 1990 ≥ 5 *cm* DBH	Mortality (%)	X^2	P
Anisoptera costata	L	14	14	0.00	-	-	8	8	0.00	-	-
Anisoptera laevis	L	73	70	4.11	-	-	64	62	3.12	-	-
Anisoptera megistocarpa	L	44	41	6.82	-	-	9	9	0.00	-	-
Dipterocarpus cornutus	M	972	941	3.19	27.62	<0.001	503	495	1.59	8.31	<0.01
Dipterocarpus costulatus	M	506	496	1.98	23.20	<0.001	120	117	2.50	0.83	>0.25
Dipterocarpus crinitus	M	165	161	2.42	6.42	<0.05	71	68	4.23	-	-
Dipterocarpus kunstleri	M	53	51	3.77	-	-	22	22	0.00	-	-
Dipterocarpus sublamellatus	M	2	2	0.00	-	-	2	2	0.00	-	-
Hopea dryobalanoides	L	554	515	7.04	0.32	>0.5	142	134	5.63	0.78	>0.25
Hopea mengerawan	L	316	295	6.65	0.47	>0.25	135	131	2.96	0.48	>0.25
Hopea sangal	L	12	12	0.00	-	-	6	6	0.00	-	-
Neobalanocarpus heimii	H	2800	2699	3.61	65.45	<0.001	491	481	2.04	5.54	<0.05
Parashorea densiflora	L	78	74	5.13	-	-	80	76	5.00	-	-
Shorea acuminata	L	1780	1606	9.78	11.05	<0.001	431	408	5.34	1.51	>0.1
Shorea bracteolata	L	892	818	8.30	0.48	>0.25	243	229	5.76	1.57	>0.1
Shorea dasyphylla	L	29	27	6.90	-	-	14	13	7.14	-	-
Shorea guiso	H	659	634	3.79	14.02	<0.001	61	60	1.64	-	-
Shorea hopeifolia	L	40	38	5.00	-	-	20	19	5.00	-	-
Shorea lepidota	L	866	759	12.36	26.74	<0.001	306	286	6.54	4.35	<0.05
Shorea leprosula	L	2405	1932	19.67	487.77	<0.001	612	573	6.37	7.55	<0.01
Shorea macroptera	L	1221	1129	7.53	0.04	>0.75	376	360	4.26	0.01	>0.9
Shorea maxwelliana	H	4484	4281	4.53	62.78	<0.001	1198	1152	3.84	0.30	>0.5
Shorea multiflora	L	3	3	0.00	-	-	0	0	-	-	-
Shorea ochrophloia	H	382	365	4.45	5.61	<0.05	60	59	1.67	-	-
Shorea ovalis	L	1026	924	9.94	7.42	<0.01	282	269	4.61	0.15	>0.5
Shorea parvifolia	L	1230	1026	16.59	137.70	<0.001	455	429	5.71	2.77	>0.05
Shorea pauciflora	L	1928	1814	5.91	8.47	<0.01	442	427	3.39	0.64	>0.25

(continued)

Table 2a. continued

Vatica bella	H	1366	1333	2.42	53.35	<0.001	303	296	2.31	2.59	>0.1
Vatica maingayi	H	78	72	7.69	-	-	14	14	0.00	-	-
Vatica pauciflora	H	349	338	3.15	10.08	<0.01	121	117	3.31	0.22	>0.5
Dipterocarpaceae											
All species	-	24327	22470	7.63	-	-	6591	6322	4.08	-	-
19 commonest species at lower diameter	-	23901	22066	7.68	-	-	-	-	-	-	-
16 commonest species at higher diameter	-	-	-	-	-	-	6160	5904	4.16	-	-
Whole plot	-	266614	256143	3.93	-	-	68626	66331	3.34	-	-

mortality of dipterocarps of ≥ 10 *cm* DBH was lower at 1.83% y^{-1} than the plot value of 2.07% y^{-1}.

Nineteen species had an initial population of more than 100 individuals in the 1 to < 5*cm* DBH class (Table 2a). Of these, the five light hardwoods with whole population mortality rates significantly higher than the dipterocarp population rate (see previous section) suffered significantly higher mortality at this size class than the rate of 7.68% for the family of these 19 species. *Shorea leprosula, S. parvifolia* and *S. lepidota* suffered high mortalities of more than 10% each, with the rate for the first species being nearly 20%.

At this size class, the pattern of mortality for the remaining 14 species is identical to that when the entire population of each of the species is considered. The same four species had no significant difference in mortality from that of the family rate, and the remaining ten species had mortality rates significantly lower than that of the family rate. Mortality of the total population of each species was therefore reflective of mortality at the 1 to < 5 *cm* DBH class. At the ≥ 5 *cm* DBH class, 16 species had an initial population of more than 100 individuals. Only two species, *Shorea lepidota* and *S. leprosula,* had mortality rates exceeding the rate of 4.16% for the family of 16 species. The mortality rates of 12 species were not significantly different from that of the family at this size class. This list includes *S. parvifolia, S. ovalis* and *S. acuminata,* whose mortality rates were significantly higher, and *Dipterocarpus costulatus, S. maxwelliana, S. pauciflora, Vatica bella* and *V. pauciflora,* whose mortality rates were significantly lower than the family rate at the lower size class. The mortality rates of both *Neobalanocarpus heimii* and *D. cornutus* were significantly lower than that of the family rate.

Mortality rates at the 1 to < 5 *cm* and ≥ 5 *cm* DBH classes were compared for the 16 species with initial populations of more than 100 individuals at both size classes (Table 2b). In *Shorea leprosula, S. parvifolia, S. ovalis, S. lepidota, S. macroptera, S. acuminata* and *S. pauciflora,* all light hardwoods, the mortality rate in the lower size class was significantly greater than that in the higher size class, being about thrice for the first two species. The rates for the two size classes were not significantly different for each of the remaining nine species. These included four heavy hardwood species including the two commonest dipterocarps, *S. maxwelliana* and *Neobalanocarpus heimii,* two species of *Dipterocarpus,* and three light hardwood species, two of which were species of *Hopea.* Thus, turnover of stems in the small size class was of significance for the *Shorea* group of light hardwoods, and not so for the medium or heavy hardwoods.

Recruitment

For the whole plot, recruitment to the minimum size class was 1.55% of the original population (Table 3). Recruitment in the dipterocarps was significantly higher (X^2=1564.6, P<0.001) at 4.80%.

There was no recruitment in six species. These had low population levels at the initial census, and included one species each of *Anisoptera, Hopea, Vatica, Shorea,* and two species of *Dipterocarpus.*

Table 2b. Comparison of mortality rates at the 1- < 5 *cm* and ≥ 5 *cm* DBH classes for species with populations of more than 100 individuals in each class

Species	Timber density class	X^2	P
Dipterocarpus cornutus	M	3.29	>0.05
Dipterocarpus costulatus	M	0.13	>0.5
Hopea dryobalanoides	L	0.36	>0.5
Hopea mengerawan	L	2.45	>0.1
Neobalanocarpus heimii	H	3.16	>0.05
Shorea acuminata	L	8.42	<0.01
Shorea bracteolata	L	1.72	>0.1
Shorea lepidota	L	7.93	<0.01
Shorea leprosula	L	61.20	<0.001
Shorea macroptera	L	4.90	<0.05
Shorea maxwelliana	H	1.07	>0.25
Shorea ovalis	L	7.84	<0.01
Shorea parvifolia	L	33.30	<0.001
Shorea pauciflora	L	4.43	<0.05
Vatica bella	H	0.01	>0.9
Vatica pauciflora	H	0.01	>0.9

Of the 21 species, with more than 100 individuals at the initial census, *Shorea ochrophloia, S. leprosula, S. bracteolata* and *Hopea dryobalanoides* had recruitment rates significantly greater than the rate of 4.84% for the family of 21 species. Recruitment was high at more than 10% for the first two species, and the rate for the heavy hardwood, *S. ochrophloia,* was particularly high. In ten other species, recruitment rates were not significantly different from the family rate. In the remaining seven species, which included three heavy hardwoods and two medium hardwoods, recruitment rates were significantly lower than the family rate.

Change in population size

Net change in population size was computed by comparing the population at the second census, which included the recruits, with the initial population.

For the whole plot, there was a reduction in population size by 2.26%. There was also a reduction in the dipterocarp population by 2.08%.

There was no net change in population size for five species, *Anisoptera costata, Dipterocarpus sublamellatus, Hopea sangal, Shorea hopeifolia* and *S. multiflora.* These were all species with low initial population levels, and in only *S. hopeifolia* was there mortality as well as recruitment. Increase in population size was recorded for six species - *Dipterocarpus crinitus, Hopea dryobalanoides, Parashorea densiflora, Shorea guiso, S. maxwelliana* and *S. ochrophloia,* the last three being heavy hardwoods. Increase was less than 2% for all but *S. ochrophloia* which increased by more than 11%. Manokaran *et al.* (1991) had previously noted that *Hopea dryobalanoides* and the three heavy hardwood species were relatively over-represented as saplings (1 to < 5 *cm* DBH) than as adults in the initial population.

Reduction in population size was seen in the remaining 19 species, of which 12 are light hardwoods. Reduction in nine species was greater than the rate of 2.08%

Table 3. Tree recruitment in species of dipterocarp. Recruitment in species with more than 100 individuals each is compared with that of the family

Species	Timber density class	Frequency in 1987	Number recruited by 1990	Percentage recruitment	X^2	P	Frequency in 1990	Percentage change
Anisoptera costata	L	22	0	0.00	-	-	22	0.00
Anisoptera laevis	L	137	2	1.46	3.18	>0.05	134	-2.19
Anisoptera megistocarpa	L	53	2	3.77	-	-	52	-1.89
Dipterocarpus cornutus	M	1475	36	2.44	17.07	<0.001	1472	-0.20
Dipterocarpus costulatus	M	626	10	1.60	13.36	<0.001	623	-0.48
Dipterocarpus crinitus	M	236	10	4.24	0.17	>0.5	239	1.27
Dipterocarpus kunstleri	M	75	0	0.00	-	-	73	-2.67
Dipterocarpus sublamellatus	M	4	0	0.00	-	-	4	0.00
Hopea dryobalanoides	L	696	49	7.04	6.54	<0.05	698	0.29
Hopea mengerawan	L	451	16	3.55	1.49	>0.1	442	-2.00
Hopea sangal	L	18	0	0.00	-	-	18	0.00
Neobalanocarpus heimii	H	3291	85	2.58	33.66	<0.001	3265	-0.79
Parashorea densiflora	L	158	10	6.33	0.69	>0.25	160	1.27
Shorea acuminata	L	2211	77	3.48	8.08	<0.01	2091	-5.43
Shorea bracteolata	L	1135	83	7.31	13.43	<0.001	1130	-0.44
Shorea dasyphylla	L	43	1	2.33	-	-	41	-4.65
Shorea guiso	H	720	33	4.58	0.09	>0.75	727	0.97
Shorea hopeifolia	L	60	3	5.00	-	-	60	0.00
Shorea lepidota	L	1172	50	4.27	0.75	>0.25	1095	-6.57
Shorea leprosula	L	3017	316	10.47	179.60	<0.001	2821	-6.50
Shorea macroptera	L	1597	92	5.76	2.68	>0.1	1581	-1.00
Shorea maxwelliana	H	5682	292	5.14	1.03	>0.25	5725	0.76
Shorea multiflora	L	3	0	0.00	-	-	3	0.00
Shorea ochrophloia	H	442	68	15.38	88.18	<0.001	492	11.31
Shorea ovalis	L	1308	56	4.28	0.80	>0.25	1249	-4.51
Shorea parvifolia	L	1685	58	3.44	6.54	<0.05	1513	-10.21
Shorea pauciflora	L	2370	115	4.85	0.00	>0.9	2356	-0.59
Vatica bella	H	1669	9	0.54	63.36	<0.001	1638	-1.86
Vatica maingayi	H	92	0	0.00	-	-	86	-6.52
Vatica pauciflora	H	470	10	2.13	6.98	<0.01	465	-1.06
Dipterocarpaceae								
All species	-	30918	1483	4.80	-	-	30275	-2.08
21 commonest species	-	30548	1477	4.84	-	-	29916	-2.07
Whole plot	-	335240	5197	1.55	-	-	327671	-2.26

for the family. Reduction in population size of *Shorea parvifolia* was high at more than 10% of the initial population. Populations of *S. acuminata, S. leprosula, S. lepidota,* (all light hardwoods) and *Vatica maingayi* (heavy hardwood) reduced by more than 5%.

In Table 4 we examine changes in the populations of the dipterocarps according to the timber density class. Light hardwoods, represented by 18 of the 30 species, comprised 52% of the number of stems at the initial census. Heavy hardwoods, seven species in all, comprised a high proportion of 40%, mainly due to *Shorea maxwelliana* and *Neobalanocarpus heimii* being the two commonest dipterocarps, and *Vatica bella* being a relatively common species as well. Medium hardwoods, represented entirely by the five species of *Dipterocarpus*, formed only 8% of the population.

Table 4. Changes in populations of light, medium and heavy hardwood dipterocarps

Timber density class	Frequency in 1987	Proportion of total population (%)	Number died by second census	Proportion of those died (%)	Number recruited in 1990	Proportion of those recruited (%)	Frequency in 1990	Proportion of total population (%)
Light hardwoods	16136	52.19	1600	75.26	930	62.71	15466	51.09
Medium hardwoods	2416	7.81	61	2.87	56	3.78	2411	7.96
Heavy hardwoods	12366	40.00	465	21.87	497	33.51	12398	40.95
Total	30918	100	2126	100	1483	100	30275	100

Over the short period of this study, dynamic changes in the populations of the component species resulted in a reduction of just 1%, an increase of 1%, and no discernible change in the proportions of light, heavy and medium hardwoods respectively in the population of dipterocarps. Manokaran (1988) examined sapling and tree populations of all species in a 2-*ha* plot in a lowland dipterocarp forest in Sungei Menyala, and found that the light and heavy hardwood components of the populations were remarkably stable over a 32-*y* period.

Discussion

The large-scale plot at Pasoh Forest Reserve has provided us with an unique opportunity to examine dynamic changes in tree populations in a dipterocarp forest to a level as low as one centimetre diameter. It has also provided us with the opportunity to examine these changes in individual species, a large proportion of which are for the first time represented by a sufficient sample size. Manokaran and Kochummen (1987), for example, found difficulty in testing significant changes in density of species in a 2-*ha* plot over a 34-*y* period because most had few trees.

In dipterocarp forests, if not in most everwet forests, dynamics studies on juvenile trees, such as those by Barnard (1954, 1956), Wyatt-Smith (1966), Fox (1972), Becker (1983), Lieberman and Lieberman (1987), Manokaran (1988) and

Turner (1990), have only been for seedlings and in small plots as well. However, in one study in evergreen rain forest in the Solomon Islands, Whitmore (1974) reported observations for whole populations of seedlings, saplings and adults, of 12 canopy species for 6.6 years in plots totalling 13.4 *ha* in extent. Observations still continue.

Over the short term of this study, significantly higher mortality was seen in the 1 to < 5 *cm* DBH class than in the ≥ 5 *cm* DBH class for both the family of Dipterocarpaceae and the entire woody flora of the plot. For both these groups, about 80% of the total stems are in this size class, and the population structures conform to the typical reversed J-shaped curve, suggesting a stable size class distribution (Manokaran *et al.* 1991). Heavier mortality at this level will set the stage for only a proportion of the juvenile population attaining mature size to occupy the limited space available in the forest.

There was significantly higher mortality in the dipterocarps as a whole than for the whole woody flora at both size classes, but at a higher size class of ≥ 10 *cm* DBH, mortality rates were similar. These results suggest that at the understorey level where competition for light especially is greatest, the dipterocarp population is highly vulnerable but that once a certain size is reached, mortality rates decline. Manokaran (1988), for example, found that for the same forest, mortality of dipterocarps of ≥ 10 *cm* DBH over a 13-*y* period in 8 *ha* was in fact lower than the plot value.

Rainfall data do not suggest any unusual climatic changes during the period of study that could have resulted in unusully severe mortality in the plot at Pasoh. In a similar 50-*ha* tropical moist forest plot on Barro Colorado Island in Panama, Hubbell and Foster (unpublished) found large changes in absolute abundance (greater than 10%) in 40% of all species even though the intercensus interval was just three years, and attributed this to the severe drought of the 1982 to 1983 El Nino year. In contrast, Lieberman *et al.* (1985) did not observe such a 1982 to 1983 El Nino drought effect on tree mortality in a tropical wet forest at La Selva, Costa Rica.

Higher mortality of the dipterocarps was offset by significantly higher recruitment into the minimum size class, a rate thrice that of the plot rate. This is evidence of a relatively large sapling bank from which recruitment is being effected into the minimum diameter class. The Dipterocarpaceae is the second largest family in the plot in density of stems ≥ 1 *cm* diameter, exceeded only by Euphorbiaceae, (Kochummen *et al.* 1990, Manokaran *et al.* 1991), and the relatively high recruitment rate, and the expectation of an existing large sapling bank, is therefore not surprising.

At the species level several differences in behaviour were evident. *Shorea leprosula, S. parvifolia, S. lepidota, S. acuminata, S. ovalis,* and *S. bracteolata,* with large populations of more than 1000 individuals each, suffered the highest mortalities. This was clearly evident at the 1 to < 5 *cm* DBH class, and most of these species suffered high mortalities at the ≥ 5 *cm* DBH class as well. In the first five species, as well as in *S. macroptera* and *S. pauciflora,* mortality was significantly higher in the smaller size class than in the larger. This would therefore be one group of species, all light hardwoods, that have abundant populations, are almost all widespread in the plot (see Manokaran *et al.* 1992), and suffer high mortality at the sapling stage. *Hopea dryobalanoides* and *Parashorea densiflora*, with lower population levels than this group of *Shorea*, could also be included in this group as having high mortality and recruitment rates. Cousens (1965) referred to these species as the early seral components of the primary forest, and Wyatt-Smith (1954, 1963b) as well as Cousens (1965) considered *S. leprosula, S. parvifolia* and *S. macroptera* to be vigorous, aggressive species common in young regenerated forest.

S. leprosula among the light hardwoods suffered exceedingly high mortality but was also recruited into the minimum diameter class at a high rate. Thus, this species stands out as the most dynamic of the dipterocarps in the plot.

We do not have evidence to show that light hardwoods produce more offspring than heavy hardwoods other than the knowledge that *Shorea maxwelliana* fruits less frequently and *Neobalanocarpus heimii* fruits more frequently than the *Shorea* species of light hardwood. The presence of relatively large populations of several of these light hardwood species, especially at the 1 to < 5 *cm* DBH class, suggests that while these species may not be as shade tolerant as species of heavy hardwood, light conditions in the forest undergrowth at Pasoh may be sufficient for survival of relatively large numbers of seedlings, and growth to sapling stage - hence the high recruitment rates. Pasoh, as we discuss in greater detail later, has suffered high mortality of trees in recent years, and the understorey is well lit in many places in the 50-*ha* plot.

The heavy hardwood species of *Shorea, Vatica* and *Neobalanocarpus heimii*, and the medium hardwood, *Dipterocarpus* species, suffered low mortalities. This was clearly evident in the 1 to < 5 *cm* DBH class. Thus, in the understorey of the forest, saplings of these species were able to survive shade much better than saplings of the light hardwoood species. Turner (1990) found *S. multiflora*, a light hardwood, to be a highly shade tolerant species, with low mortality at the seedling stage. *Hopea nervosa*, a light hardwood in Peninsular Malaysia, but classified as medium hardwood in Sabah (Burgess 1966), was found by Brown and Whitmore (1992) to have lower mortality at the seedling stage than the light hardwoods, *Parashorea malaanonan* and *S. johorensis.*

Most of these medium and heavy hardwood species in this study had low mortalities in the larger size class as well, with rates not significantly different between the two size classes. Unlike light hardwood species, most heavy and medium hardwoood species are considered slow growing, responding only slowly to increased light exposure (Barnard 1954, Wyatt-Smith 1963a, 1963b). However, Brown and Whitmore (1992) concluded from a study in lowland dipterocarp forest in Sabah, Malaysia, that for seedlings, the most important determinant of survival and growth was size at the time of gap creation, regardless of species.

In recruitment into the minimum diameter class, behaviour of the medium and heavy hardwood species was variable. Rates were low in the *Dipterocarpus* species, *Vatica* species and in *Neobalanocarpus heimii*, but moderate in the balau group of *Shorea* with the exception of *S. ochrophloia* that had an extremely high rate. This last species, not unusually abundant in the plot, must have had a relatively large sapling bank below the minimum DBH level between the two census periods, and favourable conditions must have allowed for the relatively large recruitment level.

Thus, the group of *Dipterocarpus* species could be said to be a relatively stable group, with low mortality and recruitment rates, and the same could be said of *Neobalanocarpus heimii* and the *Vatica* species. The balau group of *Shorea* could be considered to behave differently with low mortality rates and moderately higher recruitment rates. This general observation is borne out in the values in net change in populations - the balau group of *Shorea* shows increase in population size, whereas the other medium and heavy hardwood species, with the exception of *Dipterocarpus crinitus,* show a slight decrease in population size.

More dynamic changes in the population of the light hardwood species did not translate into changes in its total frequency. The proportions in the frequencies of the light, medium and heavy hardwood species had hardly changed at the recensus. Manokaran (1988) found that the light and heavy hardwood components of the sapling and tree flora in another lowland dipterocarp forest at Sungei Menyala had remained remarkably stable over a 32-*y* period. This was despite the fact that the 2-*ha* plot in that forest experienced a relatively high mortality rate of 2.03% y^{-1} for trees ≥ 10 *cm* DBH with an expected high incidence of canopy opening. He concluded therefore that only large-scale destruction by wind on the scale that flattened a large area of lowland forest in the northeastern state of Kelantan in 1880 (Browne 1949, Wyatt-Smith 1954) or by forest exploitation (see Cousens 1958) will be necessary to change the composition of the forest altogether.

Pasoh Forest Reserve has experienced relatively high mortality of trees in recent years. Tree falls appear more common than they were before. Mortality rate over the interval 1971 to 1984 for trees of ≥ 10 *cm* DBH in four 2-*ha* plots was computed to be 2.07% y^{-1}, with a decline of 7.7% in basal area (Manokaran 1988). Because of the high density of very small trees, low density of larger trees, a rather open canopy, an irregular profile, and an understorey that is well lit in many places in the 50-*ha* plot, Manokaran and LaFrankie (1990) concluded that the forest may be regenerating on a relatively quick gap cycle, and a rapid turnover may account for the rich stocking of saplings and treelets. The repeat census scheduled for 1995 is likely to provide further insight into the regeneration process of the forest.

Conclusions

The family Dipterocarpaceae underwent more rapid turnover, mainly in the 1 to < 5 *cm* class, of saplings and trees compared to the entire woody flora in the large-scale plot. This is obviously a consequence of the total plot flora being dominated by many stems of very shade-tolerant understorey trees and shrubs at that size class.

Three different categories of dynamic changes were recognised in the species of dipterocarp. In one, shown by the abundant light hardwood *Shorea* species and a less abundant species each of *Hopea* and *Parashorea,* there was high mortality compensated by high recruitment, and *Shorea leprosula* was the most dynamic of these species. In a second category, shown by the medium hardwood species of *Dipterocarpus* and the heavy hardwood species of *Vatica* as well as by *Neobalanocarpus heimii*, mortality and recruitment rates were low. In the third category, the balau group of *Shorea* of heavy hardwoods showed low mortality rates and moderately higher recruitment rates, with the exception of *S. ochrophloia* which had an extremely high recruitment rate. These three strategies in the dipterocarps at Pasoh Forest Reserve are obviously related to the degree of response of the individual species to light conditions under the forest canopy which has become rather open because of relatively high mortality of trees in recent years. Repeated censuses scheduled at 5-y intervals will further elucidate the behaviour of the individual species.

Acknowledgements

The large-scale forest plot at Pasoh Forest Reserve is an ongoing project of the Malaysian Government, initiated by the Forest Research Institute Malaysia through its Director General, Salleh Mohd. Nor, and under the leadership of N. Manokaran, P. S. Ashton and S. P. Hubbell. Supplemental funding is very gratefully acknowledged from the following sources: National Science Foundation (USA) BSR Grant No. INT-84-12202 to Harvard University through P. S. Ashton and S. P. Hubbell; Conservation, Food and Health Foundation, Inc. (USA); United Nations, through the Man and the Biosphere programme, UNESCO-MAB grants Nos. 217.651.5, 217.652.5, 243.027.6, 213.164.4, and also UNESCO-ROSTSEA grant No. 243.170.6; and the continuing support of the Smithsonian Tropical Research Institute (USA), Barro Colorado Island, Panama. Dasima Ramudin typed the manuscript of this paper.

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