



<b>Title</b>	<b>Flora and Reproductive Phenology of the Rain Forest at Bukit Timah, Singapore</b>
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<b>Citation</b>	<b>Journal of Tropical Ecology, 1990, v. 6 n. 1, p. 55-63</b>
<b>Issued Date</b>	<b>1990</b>
<b>URL</b>	<b><a href="http://hdl.handle.net/10722/53349">http://hdl.handle.net/10722/53349</a></b>
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# Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore

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**ABSTRACT.** The 71 ha Bukit Timah Nature Reserve contains the largest surviving area of primary rain forest in Singapore. The recorded vascular plant flora of the forest consists of at least 854 species: 787 angiosperms in 109 families, 65 pteridophytes and three gymnosperms. 58.6% of the species are trees or shrubs, 18.7% climbers, 12.3% terrestrial herbs, 8.8% epiphytes and hemi-epiphytes, 1.0% saprophytes and 0.6% parasites. The four families with most species - Rubiaceae, Euphorbiaceae, Orchidaceae and Moraceae - account for a quarter of the angiosperm flora but contribute few large trees. Community reproductive phenology is characterized by supra-annual bursts of general flowering and fruiting, contrasting with a low background level. After an exceptionally dry and sunny February, 1987, more than 150 species in 42 families flowered between late March and late May, followed by an equally well-defined fruiting peak 13 weeks later, between late June and late August.

**KEY WORDS:** diversity, flowering, fruiting, phenology, rain forest, Singapore, South-east Asia.

## INTRODUCTION

The Republic of Singapore lies just north of the equator at the southern tip of the Malay Peninsula, from which it is separated by shallow straits, 0.6 km wide at the narrowest point. It has a typical equatorial climate with a mean annual rainfall in the study area of 2579 mm and no month with a mean rainfall of less than 140 mm. Singapore is one of the least seasonal places in the world (Walter *et al.* 1975). Ninety-five per cent of the original forest cover was cleared during the nineteenth century and today more than half the island is urban in character. The largest surviving area of primary forest is in the 71 ha Bukit Timah Nature Reserve on the slopes and summit of Singapore's highest hill, Bukit Timah (163 m). The history and current status of this reserve is described in detail in Corlett (1988). Only about 60% of the area is primary forest and most of this has been considerably disturbed in the past. The rest is secondary forest of various ages. However, except along the margins of roads and other artificial openings, there has been no invasion of exotic or native weedy species and the rain forest flora seems largely intact.

The reserve has been studied for many years by local biologists but little work has been published. Exceptions include the ecology of forest invertebrates

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(Murphy 1973), a survey of the large trees (Wong 1987), and a popular guide-book (Singapore Science Centre 1985). This paper reports two separate investigations in the forest: the composition by family and habit of the vascular plant flora and an account of an episode of mass flowering and fruiting in 1987. Plant names in the text follow Keng (1973-85).

#### METHODS

I have been visiting Bukit Timah at least once a month since January 1984. Between January 1986 and November 1987, I made weekly visits to record plants in flower or fruit. Between July 1986 and November 1987, flowering and fruiting were recorded on a semi-quantitative basis by scanning the ground over an approximate 2 m width along a 5.1 km route through the forest. An individual tree (or climber) was described as flowering or fruiting only if fresh flowers or ripe fruits, or parts of them, were present on the ground beneath. Flowers in very small numbers in relation to tree size were ignored. This method of data collection is an economical way of investigating community phenological patterns. The alternative of repeated observations on marked trees (Medway 1972, Ng 1977, 1981) gives more detailed individual and species phenologies but limits the number of species that can be followed. The route consisted of roadsides and forest paths in order to minimize fresh disturbance to the reserve. Although there was usually a continuous tree canopy overhead, light-demanding species are over-represented in the records. Two of these - *Pellacalyx saccardianus* (Rhizophoraceae) and *Pternandra echinata* (Melastomataceae) - were so abundant that they were excluded from the counts.

The vascular plant list for the reserve was compiled from three sources: the species seen during my visits to the reserve, identified where necessary by comparison with specimens in the herbarium of the Singapore Botanic Garden; a thorough search of the same herbarium for specimens collected at Bukit Timah during the last hundred years; and a search of the taxonomic literature for references to specimens collected at Bukit Timah. Species confined to artificial openings, highly disturbed areas, and the forest margins were excluded as far as possible, but it is probable that the final list includes some species, particularly of herbs and climbers, that were not part of the original rain forest flora. Bukit Timah has been intensively collected since the 1880s so the plant list is likely to be as complete as any in the region, although some species may now be extinct. Significant numbers of omissions are most likely among the epiphytes and lianas. The list will be published elsewhere after it has been checked.

#### RESULTS

##### *Flora*

Table 1 summarizes the composition of the vascular plant flora by family (with all pteridophyte families combined) and major habit types. All angiosperm

Table 1. Vascular plant flora of Bukit Timah by family and life-form. Rank order for each life-form indicated in parentheses.

Family	Trees and shrubs	Climbers	Herbs	Epiphyte and hemi-	Others	Total
Pteridophytes	3	7	29 (1)	26 (1)	—	65
Gnetaceae	—	3	—	—	—	3
Rubiaceae	37 (2)	16 (2)	3	3	—	59
Euphorbiaceae	57 (1)	—	—	—	—	57
Orchidaceae	—	—	18 (2)	24 (2)	5*	47
Moraceae	21	4	—	12 (3)	—	37
Annonaceae	25 (4)	11	—	—	—	36
Palmae	11	19 (1)	—	—	—	30
Myrtaceae	26 (3)	—	—	—	—	26
Leguminosae	14	10	—	—	—	24
Lauraceae	22 (5)	—	—	—	—	22
Araceae	—	9	12 (3)	—	—	21
Melastomataceae	11	5	2	2	—	20
Guttiferae	19	—	—	—	—	19
Dipterocarpaceae	18	—	—	—	—	18
Myristicaceae	17	—	—	—	—	17
Fagaceae	12	—	—	—	—	12
Sapotaceae	12	—	—	—	—	12
Anacardiaceae	11	—	—	—	—	11
Apocynaceae	4	7	—	—	—	11
Burseraeae	11	—	—	—	—	11
Elaeocarpaceae	11	—	—	—	—	11
Meliaceae	11	—	—	—	—	11
Sterculiaceae	10	1	—	—	—	11
Vitaceae	—	9	—	—	—	9
Asclepiadaceae	—	2	—	6	—	8
Cyperaceae	—	—	8	—	—	8
Ebenaceae	8	—	—	—	—	8
Myrsinaceae	4	4	—	—	—	8
Sapindaceae	8	—	—	—	—	8
Polygalaceae	7	—	—	—	—	7
Theaceae	7	—	—	—	—	7
Zingiberaceae	—	—	7	—	—	7
Celastraceae	3	3	—	—	—	6
Connaraceae	1	5	—	—	—	6
Pandanaceae	3	3	—	—	—	6
Piperaceae	—	6	—	—	—	6
Loganiaceae	2	4	—	—	—	6
Dilleniaceae	4	1	—	—	—	5
Flacourtiaceae	5	—	—	—	—	5
Loranthaceae	—	—	—	—	5†	5
Rutaceae	5	—	—	—	—	5
Thymelaeaceae	3	2	—	—	—	5
Bombacaceae	4	—	—	—	—	4
Dioscoreaceae	—	4	—	—	—	4
Dracaenaceae	4	—	—	—	—	4
Gesneriaceae	1	1	1	1	—	4
Menispermaceae	—	4	—	—	—	4
Olcaceae	4	—	—	—	—	4
Poaceae	—	—	4	—	—	4
Rhizophoraceae	4	—	—	—	—	4
Verbenaceae	4	—	—	—	—	4
59 other families	59	20	19	1	4*	103
Total angiosperms	498	150	76	49	14	787
Total vascular plants	501	160	105	75	14	855
Percentages	58.6	18.7	12.3	8.8	1.6	

\* Saprophytes.

† Parasites.

families represented by four or more species are listed and the rank order for each habit type indicated in parentheses. Trees and shrubs together make up 58.6% of the flora, climbers 18.7%, terrestrial herbs 12.3%, and epiphytes and hemi-epiphytes (the latter all figs) 8.8%. There were also nine terrestrial saprophytes (1.0%) and five crown parasites (0.6%). The angiosperm flora is extremely diverse, consisting of 787 species in 109 families. The four largest families - Rubiaceae, Euphorbiaceae, Orchidaceae and Moraceae - account for a quarter of this flora. However, a ranking by cover or biomass would be very different. The orchids contribute negligible biomass and the Rubiaceae and Moraceae contain few large trees. The results of Wong (1987), after exclusion of secondary forest and planted species, show that the family Dipterocarpaceae dominates the large tree (>19.4 cm diameter at breast height) component, in terms of individuals, while the Euphorbiaceae has most species. Two dipterocarps, *Shorea curtisii* and *Dipterocarpus caudatus*, are the commonest large trees, followed by *Gluta wallichii* (Anacardiaceae).

### Reproductive phenology

Figure 1 shows the numbers of species and individuals in flower and fruit along the 5.1 km phenology route from July 1986 to November 1987. Repro-

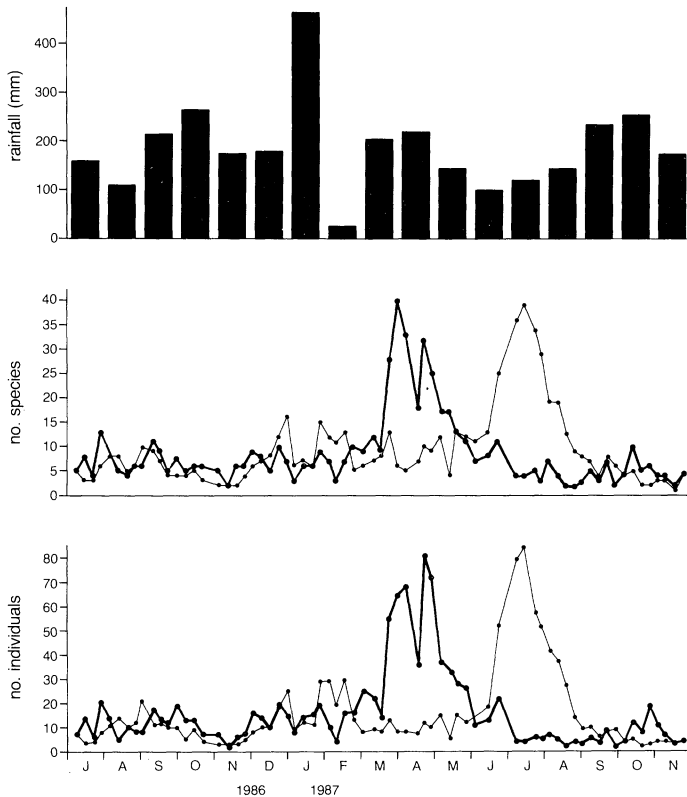


Figure 1. Monthly rainfall and numbers of species and individuals in flower (thick line) and fruit (thin line) along a 5.1 km route through the forest at Bukit Timah, between July 1986 and November 1987.

ductive activity was minor for most of this period, with a mean of 6.1 species and 10.3 individuals flowering, and 6.9 species and 10.2 individuals fruiting, outside the periods of mass flowering and fruiting. However, the cumulative total number of species flowering and fruiting outside the peak period was similar to the total within it (Appendix 1). Although I have no quantitative data, these figures are probably typical for the period January 1984 to July 1986 as well.

The episodes of mass flowering and mass fruiting were equally well-defined and each lasted two months, from late March to late May and from late June to late August 1987, respectively. The maximum correlation between flowering and fruiting, for both species and individuals, occurred with an offset of 13 weeks, suggesting that this is the mean period of fruit development. The mass flowering episode had two peaks and the maximum number of species in flower (40) and individuals in flower (81) occurred at different times. There was a single fruiting peak, with a maximum of 39 species and 84 individuals. Altogether, more than 150 species in more than 42 families (including species not on the phenology route) flowered and fruited during this period. This included emergent, canopy, sub-canopy and understorey trees and shrubs as well as climbers: both light-demanding and shade-tolerant species. Moreover, the mass fruiting episode involved both wind-dispersed species (e.g. *Dipterocarpus*, *Shorea*, *Gluta*, *Heritiera*, *Kokoona*) and the full range of animal-dispersed fruit types, including typical primate (*Artocarpus*, *Garcinia*), bat (*Elaeocarpus*, *Palaquium*), and bird (*Litsea*, *Myristica*, *Santiria*, *Timonius*) dispersed genera. Many species had not reproduced before in 1986 or 1987, but some frequently-reproducing species (e.g. *Timonius wallichianus*) had a reproductive maximum at this time. There were no clear cases of sequential flowering in related species, as observed elsewhere (Appanah 1985). Appendix 1 lists species which reproduced on the phenology route only during the mass flowering and fruiting episode, both during and outside it, or only outside it. Only species that I am fairly confident were consistently identified throughout the study are included.

#### DISCUSSION

There are no published complete species lists for any rain forest area in South-east Asia and most forest surveys have concentrated on large trees. The Orchidaceae, Rubiaceae and Euphorbiaceae, in that order, are the largest families in the Malayan flora as a whole (Whitmore 1973), suggesting that Bukit Timah is typical in this respect. The Bukit Timah forest can be classified as 'Coastal Hill Dipterocarp Forest' (Symington 1943, Whitmore 1984) because of the presence of species such as *Shorea curtisii*, otherwise confined to altitudes above 225 m in the main ranges. The occurrence of *Shorea curtisii*, with its characteristic hard, waxy leaves, on coastal hills has been attributed to the high rate of evaporation caused by constant unsaturated sea breezes (Whitmore 1984) and this may also influence other aspects of the flora, and account for the apparent paucity of epiphytes at Bukit Timah.

Gentry & Dodson (1987) give the habit composition of complete local florulas of similar size at five Neotropical rain forest sites. The three moister sites (Jauneche, Ecuador - rainfall 1855 mm; Barro Colorado, Panama - 2670 mm, but with a marked dry season; Rio Palenque, Ecuador - 2980 mm) had similar percentages of climbers (16-20%) and parasites (1%) in the flora but differed significantly in the other components. The contribution of epiphytes ranged from 11% for Jauneche, which is considerably drier than Bukit Timah, to 22% (or 30% 'if disturbed habitat species are excluded') for the wettest site, Rio Palenque. Comparisons for the other components are hindered by differences in the classification of habit types: Gentry & Dodson included 'subshrubs' with herbs while I classified all such plants as herbs or 'trees and shrubs', since I had insufficient habit information for many species. However, the difference between the 12% of herbs at Bukit Timah and the 33-36% at the three Neotropical sites is too large to explain by a difference in classification. The dominance of woody over herbaceous habits in the species composition at Bukit Timah may be a distinctive feature of South-east Asian rain forests.

The phenomenon of massive, irregular, supra-annual 'general flowering' in the lowland dipterocarp forests of west Malesia is well known but rather poorly documented. The 1987 episode at Bukit Timah was similar to, but briefer and more clearly defined than, previous episodes described in the Malay Peninsula (Appanah 1985, Medway 1972, Ng 1977, Raemaekers *et al.* 1980). There seems to be no equivalent event in the everwet parts of Africa and the Neotropics, where flowering and fruiting are more regular and more evenly distributed in time (Frankie *et al.* 1974).

Suggested environmental cues for mass-flowering in South-east Asia include dry weather (Foxworthy 1932, Medway 1972) and increased daily sunshine hours (Ng 1977). In 1987, Bukit Timah experienced an exceptionally dry (Figure 1) and sunny February. Between 30 January and 3 March, there was only 24.5 mm of rainfall at the nearest rainfall station, 1.5 km away, compared with a February mean for 1963-86 of 178.9 mm. There was a mean of 9.23 daily sunshine hours during February at the nearest sunshine station, 25 km away, compared with a long term February mean of 6.43 hours. The most recent previous dry period of this duration occurred in 1983, when only 22.8 mm fell in February and 43.1 mm in March. This was also followed by a peak in reproductive activity, unfortunately unquantified. The more regular and intense dry seasons experienced by African and Neotropical rain forests may make detection of such supra-annual cues impossible (Janzen 1974). Appanah (1985) speculates that the trees of the lowland dipterocarp forests have retained a flowering cue evolved in more seasonal climates before migration into everwet equatorial lowlands.

A more interesting and complex question is the adaptive significance, if any, of this behaviour for the plants involved. The suggestion that 'mast fruiting' evolved as a mechanism for the satiation of seed predators, thus ensuring the escape of at least some seeds (Janzen 1974), is convincing for the dipterocarps

and other wind-dispersed species. However, a net advantage to animal-dispersed plants is hard to imagine, even allowing for the ability of some vertebrate seed-dispersers to change their diet or migrate over long distances in response to a fruit glut (Leighton & Leighton 1983). Are seed predators more easily satiated than seed dispersers?

Apart from the risk of disperser satiation in animal-dispersed species, there are also likely to be problems of pollinator availability during mass flowering in animal pollinated plants. Appanah (1985) suggests that competition for pollinators is reduced by sequential flowering among species with the same pollinators, the utilization of tiny, fast-breeding insects such as thrips as pollinators, and, in some cases, apomixis. However, these mechanisms seem unlikely to be sufficient to eliminate the expected disadvantages of mass flowering in all the species involved.

An alternative explanation is that interspecific synchronization of reproductive activity is not, in itself, advantageous. It may simply be a consequence of the need for synchronization between individuals of the same species for pollination success and the rarity of environmental cues strong enough to override local environmental variation. Interspecific synchronization would thus occur because many species use the same cue for intraspecific synchronization. Immediate objections to this hypothesis are that many species do use alternative, more frequent cues and that a shared cue need not result in interspecific synchronization of flowering and fruiting because flower and fruit development times can vary between species.

A convincing explanation for the unique reproductive phenology of the lowland dipterocarp forests of equatorial South-east Asia is only likely to come from long term studies of the entire rain forest ecosystem. Unfortunately, there may be no remaining area sufficiently large and with a sufficiently intact vertebrate fauna for such a study to be carried out.

#### ACKNOWLEDGEMENTS

I wish to thank H. Keng, Ahmed Samsuri, and H. T. W. Tan for introducing me to the flora of Bukit Timah, P. W. Lucas, C. D. Hails and D. H. Murphy for encouragement and many useful suggestions, and the Meteorological Service of Singapore for the climatic records.

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Accepted 29 September 1988

Appendix 1. Species that reproduced on the phenology route only during the mass flowering and fruiting episode, both during and outside it, or only outside it. Only species consistently identified from the beginning of the study are included. Names follow Keng (1973-85).

During	Both	Outside
<i>Alangium ridleyi</i>	<i>Agrostistachys longifolia</i>	<i>Actephila excelsa</i>
<i>Aporosa benthamiana</i>	<i>Alstonia angustiloba</i>	<i>Alangium nobile</i>
<i>Aquilaria malaccensis</i>	<i>Artocarpus elasticus</i>	<i>Antidesma coriaceum</i>
<i>Ardisia teysmanniana</i>	<i>Bhesa paniculata</i>	<i>Artabotrys suaveolens</i>
<i>Artocarpus rigidus</i>	<i>Camptospermum auriculatum</i>	<i>Bauhinia semibifida</i>
<i>Baccaurea kunstleri</i>	<i>Castanopsis wallichii</i>	<i>Calophyllum ferrugineum</i>
<i>B. parviflora</i>	<i>Clerodendrum laevifolium</i>	<i>C. pulcherrimum</i>
<i>Buchanania sessilifolia</i>	<i>Combretum sundaicum</i>	<i>C. tetrapterum</i>
<i>Cyathocalyx ridleyi</i>	<i>Cratoxylum cochinchinense</i>	<i>Canarium littorale</i>
<i>Diospyros lanceifolia</i>	<i>Cyathocalyx ramuliflorus</i>	<i>Elaeocarpus ferrugineus</i>
<i>Dipterocarpus caudatus</i>	<i>Derris thyrseiflora</i>	<i>E. mastersii</i>
<i>Dysoxylum cauliflorum</i>	<i>Durio griffithii</i>	<i>E. nitida</i>
<i>Eurycoma longifolia</i>	<i>Elaeocarpus petiolatus</i>	<i>Embelia ribes</i>
<i>Ganua kingiana</i>	<i>Endospermum diadenum</i>	<i>Garcinia griffithii</i>
<i>Gonystylus maingayi</i>	<i>Euodia glabra</i>	<i>Gironniera parvifolia</i>
<i>Heritiera simplicifolia</i>	<i>Gaertnera grisea</i>	<i>Glycosmis chlorosperma</i>
<i>Irvingia malayana</i>	<i>Garcinia parvifolia</i>	<i>Gnetum microcarpum</i>
<i>Ixonanthes icosandra</i>	<i>G. scortechinii</i>	<i>Guoia pubescens</i>
<i>Knema latericia</i>	<i>Gluta wallichii</i>	<i>Gynotroches axillaris</i>
<i>Kokoona reflexa</i>	<i>Gomphia serrata</i>	<i>Hopea mengawaran</i>
<i>Lithocarpus enclisacarpus</i>	<i>Gordonia singaporeana</i>	<i>Knema intermedia</i>
<i>Litsea singaporeana</i>	<i>Grewia blattaefolia</i>	<i>Lindera lucida</i>

## Appendix 1-continued

During	Both	Outside
<i>Lophopetalum wightianum</i>	<i>Guoia pubescens</i>	<i>Litsea elliptica</i>
<i>Macaranga gigantea</i>	<i>Ixonanthes reticulata</i>	<i>Litsea grandis</i>
<i>M. trichocarpa</i>	<i>Koompassia malaccensis</i>	<i>Mezzettia leptopoda</i>
<i>Maranthes corymbosa</i>	<i>Litsea firma</i>	<i>Neesia altissima</i>
<i>Memecylon minutiflorum</i>	<i>Macaranga triloba</i>	<i>Poikilospermum suaveolens</i>
<i>Myristica cinnamomea</i>	<i>Magnolia elegans</i>	<i>Prunus polystachya</i>
<i>Myristica</i> sp. 2	<i>Ochanostachys amentacea</i>	<i>Pyrimidanthe prismatica</i>
<i>Notaphoebe umbelliflora</i>	<i>Parkia speciosa</i>	<i>Rourea minor</i>
<i>Palaquium microphyllum</i>	<i>Palaquium gutta</i>	<i>Urophyllum streptopodium</i>
<i>Payena lucida</i>	<i>Pellacalyx saccardianus</i>	<i>Willughbeia coriacea</i>
<i>Pentace triptera</i>	<i>Planchonella maingayi</i>	
<i>Phaeanthus ophthalmicus</i>	<i>Polyalthia sumatrana</i>	
<i>Pimeleodendron griffithianum</i>	<i>Pternandra echinata</i>	
<i>Popowia fusca</i>	<i>Randia anisophyllea</i>	
<i>P. pisocarpa</i>	<i>Rhodamnia cinerea</i>	
<i>Prismatopteris tetranda</i>	<i>Streblus elongata</i>	
<i>Pterospermum javanicum</i>	<i>Strychnos axillaris</i>	
<i>Santiria apiculata</i>	<i>Timonius wallichianus</i>	
<i>Shorea curtisii</i>		
<i>S. parvifolia</i>		
<i>Sindora wallichii</i>		
<i>Smilax myosotiflora</i>		
<i>Spatholobus ferrugineus</i>		
<i>Tinomiscium petiolare</i>		
<i>Vatica maingayi</i>		
<i>Ventilago malaccensis</i>		
<i>Xerospermum intermedium</i>		
<i>Xylophia malayana</i>		