

Doctoral thesis

General flowering in an aseasonal tropical forest:
plant reproductive phenology and plant-pollinator interactions
in a lowland dipterocarp forest in Sarawak

非季節性熱帯雨林における一斉開花現象

サラワク低地フタバガキ林における植物繁殖フェノロジーと
植物－送粉者相互作用

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要 約

東南アジア熱帯の低地フタバガキ林では、一斉開花と呼ばれる現象が知られている。一斉開花とは、2-10年周期で林冠を構成する様々な樹種が数ヶ月の間に次々と開花・結実する現象である。この現象を調べるため、1992年からマレーシア・サラワク州・ランビル国立公園において、定期的に305種576個体の植物の開花・結実活動を記録し、分析をおこなった。その結果、1992年から1995年までは調査対象の植物のうちの開花している種、あるいは個体の割合は共に2-5%と低かったが、その割合は1996年3月から急速に上昇して20%に達し、一斉開花を記録した。開花割合の変化は5月と9月にピークをもつ二山を示した。また、一斉開花は70メートルをこす突出木から林床低木や着生ランまで多様な植物がつくり出す現象だということがわかった。

フタバガキ林の植物はそのほとんどが動物に送粉を依存しているので、一斉開花がおこると送粉者の需要が急に高くなる。普段は花資源の乏しい林で一斉開花時の送粉サービスがどのようにまかなわれているのかは、一斉開花をめぐる大きな問題の一つである。これまで、訪花昆虫の移入と林内での増殖によって送粉者が増加するという例が知られていた。本研究では、一斉開花時にしか開花しないフタバガキ科のマルバサラノキで、ハムシを含む甲虫が重要な送粉者であることを示したが、これは一斉開花時とそうでない時で食物をかえるという今まで知られていなかった送粉者供給システムを示唆するものである。

一斉開花の進化的要因については、Janzen (1974) による種子捕食者飽和仮説が知られているが、本研究ではあらたに同調が送粉効率を高めるという送粉促進仮説を提出した。それに加え、一斉開花の進化において非季節性という環境が重要な要因であった可能性が示唆された。なぜなら、非季節性熱帯には開花トリガーとして使える環境変数が少ないために、いろいろな種が同じ環境変数を開花トリガーとして採用する結果となり開花が同調した、という可能性があるからである。

今後、気象と植物繁殖フェノロジーの長期モニタリングと一斉開花という周期性の乏しい環境下での植物動物相互作用の観察が、一斉開花現象の解明にも、高い植物の多様性を誇る低地フタバガキ林の保全という面からも重要だと考えられる。

Summary

The phenomenon of 'general flowering' has been reported only from part of tropical forests in Southeast Asia. During general flowering, which occurs at irregular intervals of two to ten years, nearly all dipterocarp species together with species of other families, come heavily into flower. To investigate the phenomenon, on which no systematic studies have been made at the community level, my research team monitored 576 individual plants representing 305 species. The proportions of flowering species and individuals were low (2-5%) in 1992-1995, but increased drastically in March 1996, and reached 16.9% and 21.1% respectively in May 1996, followed by a lower peak in September, 1996. Concentration of flowering events in general flowering period (GFP) was found in plants of various taxonomic groups and life forms.

One of the most interesting and important problems is what pollination systems are adopted by these general flowering species, because such intense general flowering with irregular intervals can bring about immense demands for pollinators. Two mechanisms, immigration and multiplication of the populations within the forest have been known to supply pollinators in general flowering. An emergent tree species, *Shorea parvifolia* (Dipterocarpaceae), which flowered only in GFP, was revealed to be pollinated by beetles (Chrysomelidae and Curculionidae, Coleoptera). The beetles probably respond to an abrupt increase of floral resource in a general flowering by changing foods from dipterocarp leaves to flowers. Such a feeding niche shift in general flowering has never been reported.

A possible cause for general flowering, promotion of pollination, i.e. interspecific synchronization in flowering bring about larger pollination success, was proposed in addition to predator satiation hypothesis indicated by

Janzen (1974). On the other hand, paucity of environmental variables suitable for a flowering cue may play an important role. It obliges different plant species to adopt the same environmental variable as a flowering trigger and cause synchronized flowering among species.

Long-term monitoring of climate and plant phenology in aseasonal forests with irregular general flowering event, as well as observation of plant-animal interactions, may give the critical information on this unique phenomenon and on conservation of lowland dipterocarp forests with extremely high plant species diversity.

Chapter 1. Introduction

Plant reproductive phenology

Phenological studies address the timing of recurring biological events. For plants, these include reproductive events such as bud formation and flowering, fruiting, and seed germination, along with vegetative processes like leaf flushing and shedding. Plant phenology often has great impact on animal populations by causing temporal changes in resource availability. Phenological schedules may in turn be affected by biotic factors through competition, herbivory, pollination and seed dispersal, in addition to various climatic variables (Brody 1997; reviewed by Rathcke & Lacey 1985; van Schaik *et al.* 1993). It has been demonstrated for some plant species that reproductive success or mortality is correlated to phenological traits (e.g. for flowering, Augspurger 1981; for germination, Tevis 1958).

There has been considerable controversy concerning both ultimate and proximate causes of flowering phenologies. Phenological strategies of flowering have been thought to be formed through competition for pollinators, although significant temporal segregation of flowering among plants sharing pollinators has rarely been detected (Stiles 1977; Brown & Kodric-Brown 1979; Poole & Rathcke 1979; Wheelwright 1985; Kochmer & Handel 1986; Murray *et al.* 1987; Ollerton & Lack 1992; Wright & Calderon 1995; but see Pleasants 1980; Gleeson 1981; Armbruster 1986; Ashton *et al.* 1988). There is still little strong evidence of competition for pollinators among co-occurring species (but see Campbell 1985; Campbell & Motten 1985), and flowering may be completely out of phase with pollinator abundance (Zimmerman *et al.* 1989). On the other hand, some studies suggest that synchronized flowering of different species could facilitate pollination through increase of resource density and local pollinator attraction (Thompson 1982; Schemske 1981). There are many other possible mechanisms

that reduce competition for pollinators yet do not involve divergence in flowering time (Ollerton & Lack 1992). Kochmer & Handel (1986) and Wright & Calderon (1995) suggested that phylogenetic factors strongly affect flowering phenology and determine rough timing of flowering.

Phenology in tropical forests

In contrast with the temperate region, where clear annual cycles in plant phenology predominate, seasonal fluctuation in mean temperature is often less than fluctuation within a single day in tropical regions. Instead of temperature, periodic change in rainfall caused by movements of the intertropical convergence zone often determine seasonality (van Schaik *et al.* 1993). Dry seasons (mean monthly rainfall less than 100 mm) within an annual cycle occur in most tropical regions, and many studies have shown strong correlations between tropical plant phenology and rainfall (Borchert 1983; Murali & Sukumar 1994; Reich & Borchert 1984; Augspurger 1981).

Part of the complexity of tropical phenology is due to the differences in patterns from one level of analysis to another (Newstrom *et al.* 1994a, 1994b). Flowering phenology can be analyzed from the level of individual flowers and branches up to populations of a species and of different species in the same community. In temperate forests, behavior of an individual plant and of the population is not always distinguished because patterns tend to be similar at the level of individuals and population. This is not usually true in tropical forest. For example, individual plants may flower for a short time, but at the level of the population they may be flowering continuously. Most studies on tropical plant phenology have been directed at community-level patterns, while little attention has been paid to individual plants (see references in Newstrom *et al.* 1994b). However, phenology develops under selection pressures at the individual level. Community level patterns should be understood as the

integration of the population level patterns, which have been molded to maximize fitness of individual plants.

Lowland dipterocarp forests in Southeast Asia and general flowering

The central part in Southeast Asian tropics lack a predictable dry season (Inoue *et al.* 1993). This effectively aseasonal climate is caused by monsoons driven by the convergent airmasses from the Tibetan highlands and the world's warmest sea water in the western Pacific. A summer monsoon from the Indian ocean and winter monsoon from the Pacific and South China Sea bring rain to central Southeast Asia throughout the year.

One characteristic of the forest in the region is exceptionally high tree species diversity. In particular, the lowland mixed dipterocarp forests in Borneo are thought to be among the richest forests in tree species diversity in the world (Whitmore 1984). Dipterocarpaceae is the major component among the canopy emergent trees. Usually, several dipterocarp species and genera grow together so that a single species does not dominate.

What sort of reproductive phenology do the plant have in such an aseasonal climate ? Interestingly, the phenomenon of 'general flowering' has been reported only from this region (Wood 1956; Medway 1972; Janzen 1974; Cockburn 1975; Chan & Appanah 1980; Appanah 1985, 1993; Ashton 1989, 1993; Ashton *et al.* 1988; Corlett 1990). During general flowering, which occurs at irregular intervals of three to ten years, nearly all dipterocarp species, together with species of other families, come heavily into flower. Related species of dipterocarps may flower sequentially with high intra-specific synchrony (Appanah & Chan 1981; Appanah 1985). It is well-known by local people that a general flowering episode is reliably followed by abundant fruiting several months later. In spite of the importance and uniqueness of the general flowering phenomenon, there is no detailed study which accurately describes a

general flowering at the community level.

Pollinators during a general flowering period

General flowering phenomenon with irregular and long intervals poses questions: how the animals which live on floral resources and may be pollinators of some plants, respond to an increase of floral resources; and how the plant can receive enough pollination services in spite of great increase of demands for pollinators. Observations have been suggested some wide-ranging pollinators such as carpenter bees (*Xylocopa* species), birds, bats and giant honey bees (*Apis dorsata*) to migrate into the forest during a general flowering period (GFP). Other dwelling pollinators such as bees, wasps, butterflies also show a local increase in population density upon advance of the general flowering (Appanah 1990; Nagamitsu 1998).

The other plausible system to fill the great pollinator demand was found in beetle pollination of *Shorea* section *Mutica* (Dipterocarpaceae). These species have been known to be pollinated by thrips in Peninsular Malaysia (Appanah & Chan 1981). Once a general flowering started, thrips multiply drastically due to their short generation time, and provide sufficient pollination services for multiple species of *Shorea* (Appanah & Chan 1981). In this study, in contrast, beetles were found to pollinate *Shorea* species in addition to or rather than thrips at Lambir. The beetle pollination is different from the thrips pollination in that the beetles respond to an abrupt increase of floral resource not by increase of population but by feeding niche shift.

Objectives of the study

In this study, I explore general flowering phenomena with emphasis on plant-pollinator interactions during a general flowering period. Canopy observation system equipped with tree towers and aerial walkways enabled us

to accurately record phenology and reproductive activities of plants of various life forms (Inoue *et al.* 1995; Yumoto *et al.* 1996), as well as to observe the reproductive ecology of individual species.

After I briefly introduced characteristics of a lowland mixed-dipterocarp forest and the study site in Chapter 2, I describe plant reproductive phenology at the community level in Chapter 3. The study period covered four years and a half from August 1992 to December 1996. In Chapter 4, beetle pollination of *Shorea parvifolia* (section *Mutica*, Dipterocarpaceae) were reported as an example of important pollination system in a general flowering period. Finally, I discuss ultimate causes of general flowering and role of plant-pollinator interaction in evolution of and maintenance of this unique phenomena in lowland dipterocarp forests in Southeast Asia.

Chapter 2. Canopy observation system

Location and climate of study site

The study was carried out in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (Fig. 2-1, 4°20'N, 113°50'E, 150-250 m above sea level). The park is located about 30 km south of Miri, the capital of the Fourth Division, Sarawak, and covers an area of approximately 6949 ha (Fig. 2-

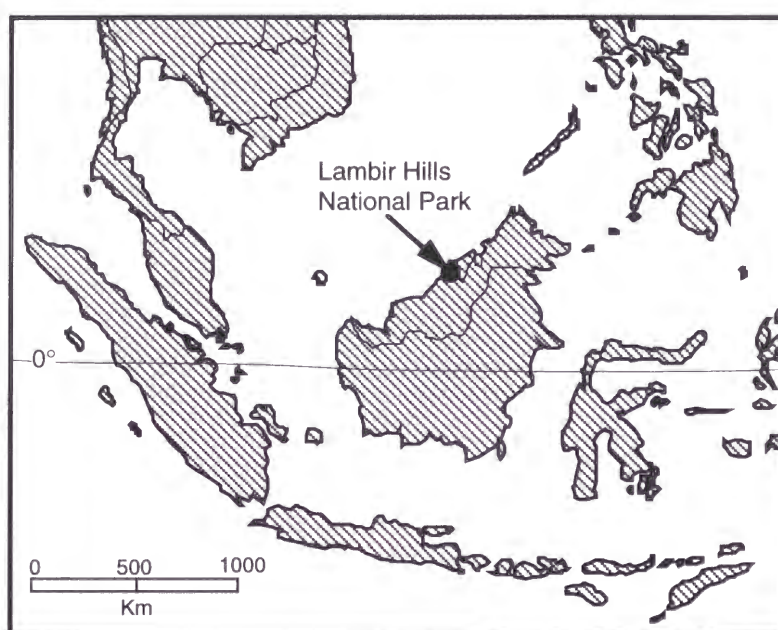


Fig. 2-1. The location of Lambir Hills National Park, Sarawak, Malaysia.

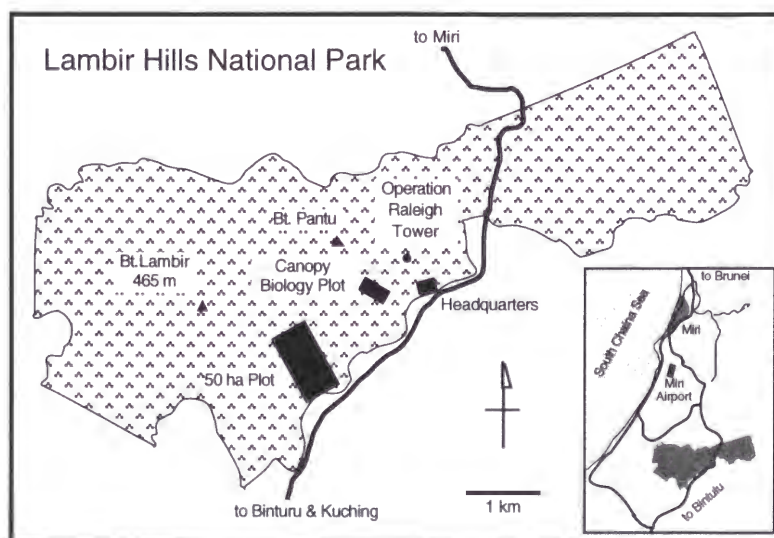


Fig. 2-2. The sites of the Canopy Biology Plot and Operation Raleigh Tower in Lambir Hills National Park (inset: Miri and surrounded areas). From Inoue & Hamid (1994).

2). Rainfall data collected for 30 years at Miri Airport, 20 km north of the research site, show that monthly rainfall fluctuate greatly up to 800 mm, and annual rainfall ranges between 2100 and 3300 mm (Fig. 2-3). Though a dryer period was observed from February to April in some years, a clear annual rhythm of rainfall is not found and mean monthly rainfall rarely falls less than mean monthly evaporation (100 mm). Daily mean temperature measured in

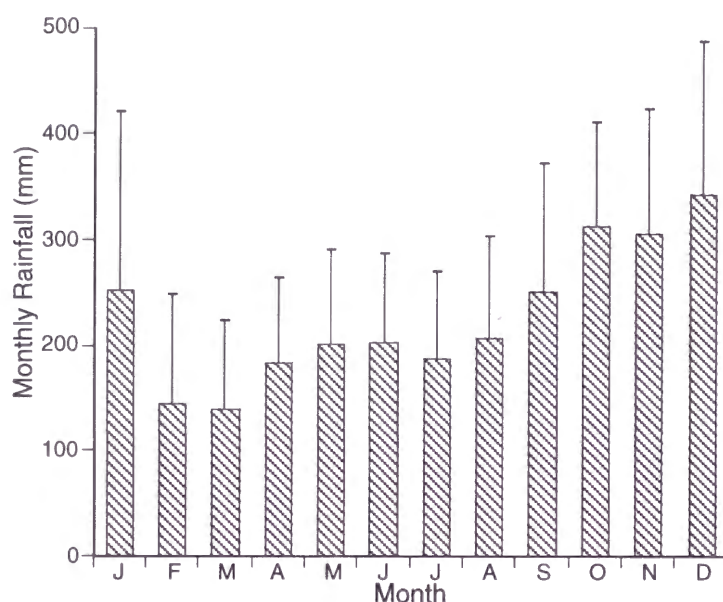


Fig. 2-3. Averaged monthly rainfall at Miri Airport from 1967 to 1996. Standard deviations are shown by bars.

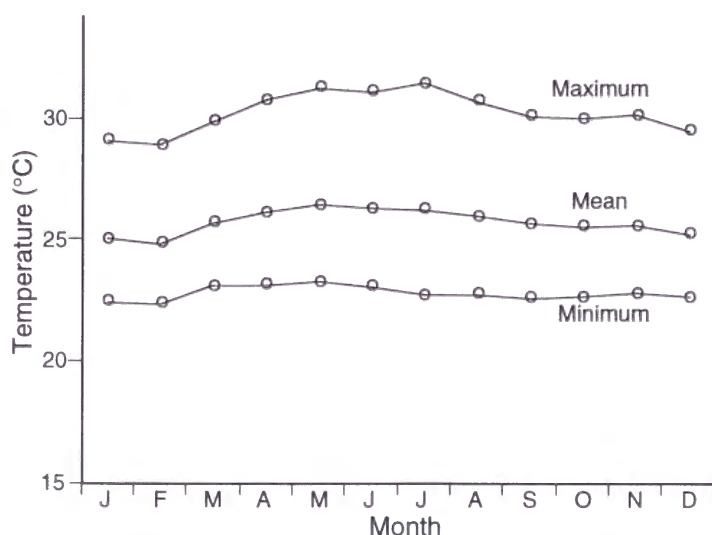


Fig. 2-4. Averaged monthly maximum, mean and minimum temperature measured on the top terrace of Tree Tower 1 in the Canopy Biology Plot from 1993 to 1996.

canopy layer of the forest is about 26 °C throughout the year, and temperature fluctuate mostly between 22 °C and 32 °C within a day (Fig. 2-4).

The most part of the park is covered by evergreen mixed-dipterocarp forests. This type of forests prevail through southwestern Sri Lanka, in Peninsular Malaysia, Sumatra, Borneo and the Philippines, and probably originally in lowland west Java (Ashton 1989). The forests are dominated by Dipterocarpaceae in the emergent layer, which sometimes reach a height of 70 m. The height is never reached in tropical forests in the other areas. The top of the forest canopy is usually very rough with cauliflower-like crowns of emergent trees, which occur as groups in the forest. All big dipterocarp trees have useful timbers. The lower layers are dominated by Euphorbiaceae, Burseraceae and Myristicaceae. The timbers and the other products including rattans (Palmae) and irripe nuts (fruit rich with fat produced by *Shorea*, Dipterocarpaceae) have been important source of revenue for government in this region.

The flora of Malesia is exceedingly rich and characterized high endemism. Censuses of tree species diversity in a particular area have been revealed that lowland forests in the region are one of the richest terrestrial ecosystem (Whitmore 1989). The great richness of flora is considered to be in part a consequence of the very complex structure of the vegetation, great tree height providing a framework and an environment within which smaller trees and plants of a wide range of life form grow (Whitmore 1984). In the park, 119 families 437 genera 1153 species of vascular plants were recognized (dicotyledons 357 genera/999 species, monocotyledons 63/130, gymnosperms 3/8, ferns and allies 15/19) by CBPS (see next section), while some plant groups are poorly collected (Nagamasu & Momose 1997). Among angiosperm families, the most diverse families were Euphorbiaceae (33 genera/101 species), followed by Dipterocarpaceae (8/83), and Rubiaceae (34/82).

The Canopy Biology Program in Sarawak

The Canopy Biology Program in Sarawak (CBPS) started in 1991 with the aim of creating new understanding of biodiversity in the canopy of tropical rainforests. In the early 1980s, productive and reproductive activities in tropical rainforests of plants were revealed to be concentrated in the canopy layer (Whitmore 1984). Though several methods and techniques to access canopy layer of the forests had been developed, CBPS adopted tree tower and walkway system to study activities of plants and animals in the canopy (Inoue & Hamid 1997).

In Lambir Hills National Park, the Canopy Biology Plot (8 ha: 200 × 400 m) and a belt transect along the waterfall trail (5 ha: 1 km × 50 m) were demarcated by CBPS (Inoue *et al.* 1995). Canopy Biology Plot included humult and udult

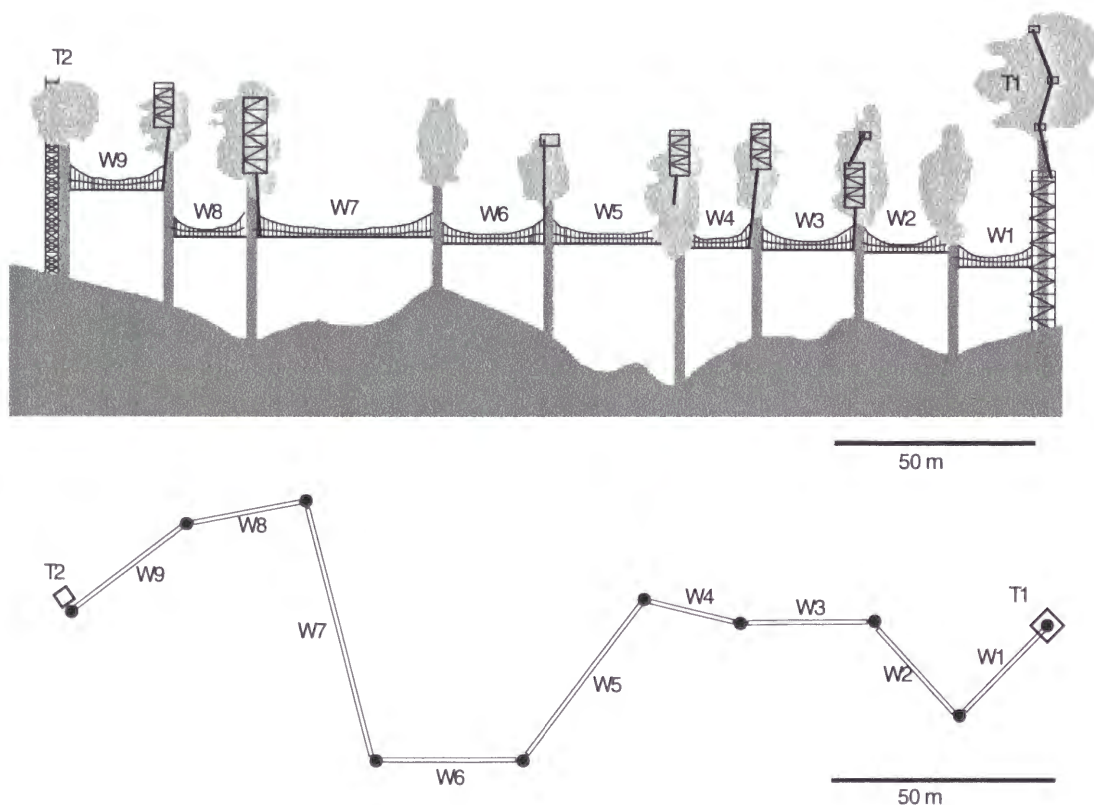


Fig. 2-5. A profile from the south (top) and top views (bottom) of Canopy Observation System in Lambir Hills National Park. From Inoue & Hamid (1994).

soils (sandy clay, light clay or heavy clay in texture), several ridges and valleys, and closed (mature-staged) forests and canopy gaps. In the mature part of this forest sample, closed canopy and subcanopy layers develop at the height between 10-40 m above the ground. Above them, crowns of emergent trees sometimes stand out above 70 m. At the center of the plot, a canopy access system consist of two tree towers and nine spans of walkways (totally 300 m long) was constructed (Fig. 2-5, Inoue *et al.* 1995; Yumoto *et al.* 1996). Tree tower 1 is constructed around an emergent dipterocarp tree (*Dryobalanops lanceolata*, Dipterocarpaceae) and 35 m high. Height of tree tower 2 is 48 m and constructed on one side of a dipterocarp tree, *Dipterocarpus pachyphyllus* (Dipterocarpaceae). The walkways penetrate the canopy or subcanopy layer, 15-35 m above the ground. The ends of each span are held either of the towers or a trunk of large tree. In addition to two towers, crowns of six trees out of the eight piers of walkways can be accessed using aluminum ladders and wooden terraces settled on the trees. The waterfall trail is located along a stream on yellow sandstone, from the headquarters of the park to the Operation Raleigh Tower (height 36 m), which is another tree tower constructed by Operation Raleigh and donated to the park.

Chapter 3. Plant reproductive phenology

Introduction

Although the importance and uniqueness of the general flowering phenomenon have been stressed by several authors (Ashton 1969; Janzen 1974; Appanah 1985, 1993; Ashton *et al.* 1988), there is no detailed study which accurately describes a general flowering at the community level, or examines the prevalence of the phenomenon among species of different life form, pollination or fruit dispersal mode. Records of gregarious flowering in most studies are restricted to Dipterocarpaceae (Burgess 1972; Ng 1977; Yap 1987; Yap & Chan 1990) or to the examination of herbarium specimens (Cockburn 1975). A few studies on general flowering have recorded reproductive phenology of plant species other than Dipterocarpaceae, but they include only a small number of individuals or species (Medway 1972; Yap 1982) or a much shorter period than one general flowering cycle (Corlett 1990).

Two studies of plant reproductive phenology, Medway (1972) and Yap & Chan (1990), covered rather long periods including more than one general flowering events. Medway (1972) monitored 61 plants of 45 species representing various families from 1960 to 1969 in Peninsular Malaysia and found that small part of observed plants flowered every year, and that most species flowered in 1963 and 1969. He suggested that the general flowering events in both the year were induced by drought. Yap & Chan (1990) reported flowering and fruiting of 16 species of *Shorea* (Dipterocarpaceae) in natural forests and plantations in Peninsular Malaysia. They found that small part of the trees flowered even in non-general flowering year, and that their fruit set in non-general flowering years was not as good as that in general flowering years. In addition, the flowering pattern was different among sites and species.

Both proximate and ultimate causes of the general flowering phenomenon have been discussed. A proximal cue of the general flowering was suggested to be a drop of daily minimum temperature by 2 °C (Ashton *et al.* 1988). Seed-predator satiation is thought to explain the interspecific mass-flowering event which leads to mast fruiting (Janzen 1974; Ashton *et al.* 1988), although there are no data demonstrating predator satiation in the forests. For further exploitation about proximate and ultimate causes for general flowering, it is important to examine characteristics of plants which take part in general flowering and climatic conditions.

In this chapter, I documents the results of monitoring individuals of as many as 305 plant species in Lambir Hills National Park, Sarawak, Malaysia from August 1992 to December 1996. At the beginning of the study, the forest was at the final stage of fruiting following a general flowering event in 1992. Thus, these phenology data comprise the first relatively complete documentation of a general flowering cycle. Besides, climatic condition was monitored just below the tree crown of an emergent dipterocarp trees. To examine flowering patterns at the individual and population levels that comprise patterns found at the community level, I define several flowering types (i.e. phenological strategies) based on the timing and frequency of flowering of individual plants. Differences in phenological strategies among life form types, pollination systems, fruit types or taxonomic groups were examined. This is an attempt to compare the phenological strategies of a wide range of plant species in the same community.

Materials and methods

Monitoring of climatic condition in the canopy

Meteorological sensors (rainfall: B-011-00; temperature/humidity: E7050-

10; solar radiation: H-205) and a data logger (M-812-Z4 of Yakogawa Weathac Corporation) were set on Tree tower 1 in May 1993 (Yumoto *et al.* 1995). The sensors and a solar battery were set on the top platform, 35 m above the ground under a tree crown of an emergent dipterocarp (*Dryobalanops lanceolata*). Data were recorded during the study at 30 minute intervals. Data were not collected during 8 August-25 September 1994, 1 June-16 June 1995, 2 May-24 May 1996 and after 29 July 1996. The rainfall data from under the tree crown underestimate the rainfall at an open area 500 m distant from the monitoring point by about 33%, as recorded by a team of Harvard University and the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute (LaFrankie, personal communication). I examined whether drops in daily minimum temperature could be a potential trigger for general flowering.

Species and life form types

Five hundred and seventy-six individual plants of 305 species in 56 families were chosen covering various plant life forms in order to monitor phenology at the community level (Table 3-1). The sampling of the plants did not directly reflect the number of individuals of each life form, but was weighted toward larger plants (e.g. canopy and emergent trees), especially in the census from the forest floor (FF). For the census from the tree towers and walkways (TW), 430 trees were observed from the canopy access system and 56 from Operation Raleigh Tower. In the census from FF, all 194 plants were observed in Canopy Biology Plot. One hundred and four plants were observed from both FF and TW. Seventy-four percent of 486 individuals in the census from TW and 98% of 194 individuals in the census from FF were non-gap trees.

We collected specimens of all accessible plants (all 194 individuals observed from FF; 282 [58%] out of 486 individuals observed from TW). When

Table 3-1. Number of genera and species in 56 plant families of plants in the Canopy Biology Plot (CBP) observed from a canopy access system in the plot (TW) and from the forest floor (FF), and plants observed from the Operation Raleigh Tower (ORT, TW). For species names under observation, see Appendix 1.

Family	No. of genera				No. of species			
	CBP		ORT	Total	CBP		ORT	Total
	TW	FF	TW		TW	FF	TW	
Anacardiaceae	5	2	4	8	7	2	4	11
Annonaceae	9	2		10	11	2		12
Apocynaceae	3			3	3			3
Aquifoliaceae	1	1		1	1	1		1
Araceae	1		1	2	1		1	2
Araliaceae	2			2	2			2
Ascrepiadaceae	2			2	2			2
Bombacaceae	2	2		2	2	3		4
Burseraceae	5	6	4	7	10	8	4	16
Celastraceae	1			1	1			1
Chrysobalanaceae	2	1		2	2	1		2
Compositae	1			1	1			1
Connaraceae	2			2	3			3
Convolvulaceae	1			1	1			1
Crypteroniaceae	1			1	1			1
Dilleniaceae	1			1	1			1
Dipterocarpaceae	6	4	5	7	35	31	11	42
Ebenaceae	1			1	2			2
Elaeocarpaceae	2			2	2			2
Euphorbiaceae	12	2	1	14	22	2	1	24
Fagaceae	2	1		2	3	1		4
Flacourtiaceae		1		1		1		1
Guttiferae	3	2	2	3	4	2	3	7
Icacinaceae	1			1	1			1
Ixonanthaceae	1		1	1	1		1	1
Lauraceae	6	5		9	6	5		9
Lecythidaceae	1	1		1	1	1		1
Leguminosae	13	4	1	13	24	8	1	25
Linaceae	1			1	1			1
Loganiaceae	1			1	1			1
Loranthaceae	2						1	3
Magnoliaceae	1						1	1
Melastomataceae	3						3	3
Meliaceae	1	1					2	1
Menispermaceae	1						1	1
Moraceae	3	2	2				3	14
Myristicaceae	4	2					4	14
Myrsinaceae	1						1	1
Myrtaceae	2	1	1				2	6
Olacaceae	2						2	2
Orchidaceae	10						2	12
Pandanaceae	1						1	1
Piperaceae	1						1	1
Rhizophoraceae	1						1	1
Rubiaceae	3						1	3
Sapindaceae	2	2					2	3
Sapotaceae	2	3					2	5
Simaroubaceae	1	2					1	2
Sterculiaceae	2	5	1				4	7
Theaceae	1						1	1
Thymelaeaceae	3						3	3
Tiliaceae	1						2	1
Ulmaceae	1						1	1
Verbenaceae	3						3	3
Xanthophyllaceae							1	1
Zingiberaceae							1	1
Unknown ^a	11						1	12
Total	89	34	19	103	152	68	26	184

^a Species whose families and species have not been identified yet.

the plant was flowering or fruiting, fertile specimens were collected and their floral characters (flowering time in a day, reward for pollinators, color and shape) were recorded. This collection of plant specimens (Plants of Sarawak, Canopy Biology Program) was identified in Sarawak Herbarium, Sarawak Forest Department. Specimens were sent to some herbaria, among which Sarawak herbarium and Herbarium of Kyoto University have a complete set (Nagamasu & Momose, 1997).

The plants were classified into eight life form types. Most tree species were distinguished by the height of the final developmental stage of reproductive individuals: 1) forest floor (max height < 2.5 m), 2) understory (2.5-12.5 m), 3) subcanopy (12.5-27.5 m), 4) canopy (27.5-42.5 m), and 5) emergent (> 42.5 m). Forest floor plants were not included in this study. I dealt with tree species that grew only at newly-made canopy gaps as 6) gap trees independently from the above five tree categories, regardless of their height. Other than trees, 7) epiphytes and 8) lianas were distinguished. Strangler figs were categorized as lianas.

Taxonomic groups (families and genera) selected for analyses in this study were: 1) Burseraceae, 2) *Dipterocarpus*, 3) *Dryobalanops*, 4) *Shorea* (Dipterocarpaceae), 5) other species of Dipterocarpaceae, 6) Euphorbiaceae, 7) Leguminosae, 8) *Artocarpus*, and 9) *Ficus* (Moraceae). These groups were among the major components of the forest. The taxonomic level of the groups (families or genera) was chosen so that their species presumably shared common reproductive characters such as pollination systems.

Pollination systems and fruit types

When flowers were found, flower visitors to and their behavior on the flowers were observed both in daytime and at night (Momose *et al.* 1998b). The

flower visitors which came in contact with both stigmas and anthers were regarded as pollinators in this paper. Vertebrate pollinators were identified in the field (for 6 plant spp.) and insect pollinators were collected as far as possible by flower beating and net sweeping (for 93 plant spp.). All insect specimens were pinned and identified to family. All bees and some beetles were identified to genus. Subfamily Apinae (honey bees and stingless bees) were identified to species. For 164 plant species at which flower visitors could not be observed or collected, the pollinator family or order was deduced from their pollination syndrome (correlation between floral characters and pollinator groups) clarified by Momose *et al.* (1998b) according to data on 270 plant species (98 spp. in this study and 172 spp. by general observations in the same study site).

This paper follows the categories of pollination systems reported by Momose *et al.* (1998b), while four bee pollination systems (*Xylocopa*, *Amegilla*, Halictidae and *Megachile*) are grouped as “solitary” bee in this study. Ten pollination systems distinguished in this study were: 1) mammal pollination (obligatorily pollinated by mammals), 2) bird pollination (obligatorily pollinated by birds, *Nectarinia jugularis*, *Arachnothera longirostra* and *A. robusta*, Nectarinidae) 3) *Apis* pollination (pollinated by *Apis dorsata*, *A. koschevnikovii* and *A. andreniformis*, Apinae), 4) small social bee pollination (pollinated by *Trigona* spp., Meliponini or *Braunsapis* spp., Allodapini, but several other insect families are also pollinators), 5) solitary bee pollination (obligatorily or dominantly pollinated by *Xylocopa* spp., Xylocopini, *Amegilla* spp., Anthophorini, Apidae, *Nomia* spp. or *Thrinchostoma* spp. Halictidae, *Megachile* spp., Megachilidae, Hymenoptera), 6) fig wasp pollination (all *Ficus* spp., pollinated by Agaonidae, Hymenoptera), 7) lepidopteran pollination (obligatorily pollinated by lepidopteran), 8) beetle pollination (obligatorily or predominantly pollinated by Chrysomelidae, Curculionidae, Nitidulidae,

Scarabaeidae), 9) diverse insect pollination (pollinated by several families or insect orders and *not dominated by any*), and 10) others (obligatorily or predominantly pollinated by thrips, flies, wasps or cockroaches). In addition to these categories, the most common pollination system, beetle pollination, is divided into two categories: Beetle pollination found in Dipterocarpaceae, and the other beetle systems. This is because the reward offered by dipterocarp flowers and the behaviors of the pollinators on the flowers were quite distinctive, and because beetles collected on dipterocarp flowers were not observed visiting any other flowers (Momose *et al.* 1998b; Chapter 4).

Three fruit types are distinguished. The species producing fruits or seeds with special rewards for vertebrate vectors, such as sarcocarps, are distinguished as animal dispersed type. The other species are classified into two categories according to the dry weight of their dispersal unit (fruits when the seeds in a fruit are dispersed altogether, or seeds when they are dispersed separately): large fruit (gravity, gyration or ballistic dispersal) and small fruit (wind dispersal) species. Large fruit species are those with the dispersal unit > 0.1 g in dry weight, irrespective of whether they have some apparatus to disperse fruits (e.g. wing) or not. The dispersal distances of seeds with heavy weight are not large, and most of them have the possibility of secondary dispersal and heavy predation by generalist seed eaters. The seeds weighing < 0.1 g are classified as small fruit, since they are easily dispersed by wind and unlikely to suffer heavy predation from generalists. In this paper, I adopt the classification based on seed weight rather than seed morphology in order to examine the predator satiation hypothesis. If satiation of generalist predators is an important factor in general flowering, differences in phenological strategies among fruit types are likely to be found.

Observation and description of phenology

From TW, plant phenology was monitored bimonthly from August 1992. This paper reports the results for 53 months up until December 1996. From April to July 1996 the census was intensified to three times a month for higher accuracy over the general flowering period (GFP). All the individuals for the census from TW had been fixed by July 1993, so that the reproductive phenology of 453 plants of 257 spp. were recorded for at least 43 months. Among the 257 spp., 175 spp. (68%) of the species were represented by a single individual, and 40 spp. (16%) and 19 spp. (7%) by two and three, respectively. Twenty-three species (9%) included more than three individuals. Data taken during the 10 months before all individuals for the census were selected, were only used in analyses of overall patterns of flowering and fruiting (Fig. 3-3) and comparisons in fruit set (Table 3-7).

In each census, the quantity of reproductive organs (flower buds, flowers, or fruits) in the crown (or on the trunk, if cauliflory) was observed with binoculars and recorded according to the following five grades; -: no flowers or fruits found; +: flowers and fruits scattered and few, or covering only a small part of the crown; 1: less than half of the crown covered with flowers and fruits; 2: flowers and fruits abundant but not distributed over the whole crown; 3: flowers and fruits covering the whole crown. The plant was defined to be “reproducing” (reproductively active) when the quantity of all reproductive organs was grade 1 or greater. Among them, the plant with any flower was defined to be “flowering”, and the plant with any mature or immature fruits was “fruiting”.

Among 486 plants observed from TW, 11 individuals were excluded from analyses because their reproductive structures were sometimes confused with their leaves. For all the 22 individuals of Moraceae and 7 individuals of other families, distinction among flower buds, flowers, immature and mature fruits

was sometimes difficult because their flower and fruit were similar in shape and/or color (e.g. syconia of *Ficus*). Data of these individuals were used when distinction between flowers and fruits was not needed. Individuals which died during the census (22 individuals) were included in the analyses of changes in percentage of flowering and fruiting individuals and comparisons of fruit set in Table 3-7, but excluded from the analyses based on classification of flowering types.

The census from FF was made monthly from August 1992 to January 1996. The plants whose flowers or fruits were found on the ground or in the crown (on the trunk, if cauliflory) were determined to be “flowering” or “fruiting” respectively.

In the both censuses from FF and TW, the records of the previous census were always referred to while making observations to help distinguish the stages of the reproductive structures. Original data were saved as text files and as SAS data sets in the Data Processing Center, Kyoto University.

Description of reproductive events

For each reproductive event, the first, peak and last observation dates of flowering were recorded (Fig. 3-1). The peak date was determined as the date when the amount of reproductive organs was at its maximum in the flowering period. If flowering continued at the same intensity for a while, I used the last census date. Observation dates of fruiting were also recorded in the same manner as flowering (Fig. 3-1). The date of the reproductive event was represented by the peak of flowering. If actual flowering was overlooked, the date that flower buds or fruits were observed was used. Such cases occurred in 153 (23%) out of the total 664 reproductive events observed. Length of flowering period in each event was defined to be the number of days between the first and last dates of flowering. If flowering was observed only once, the

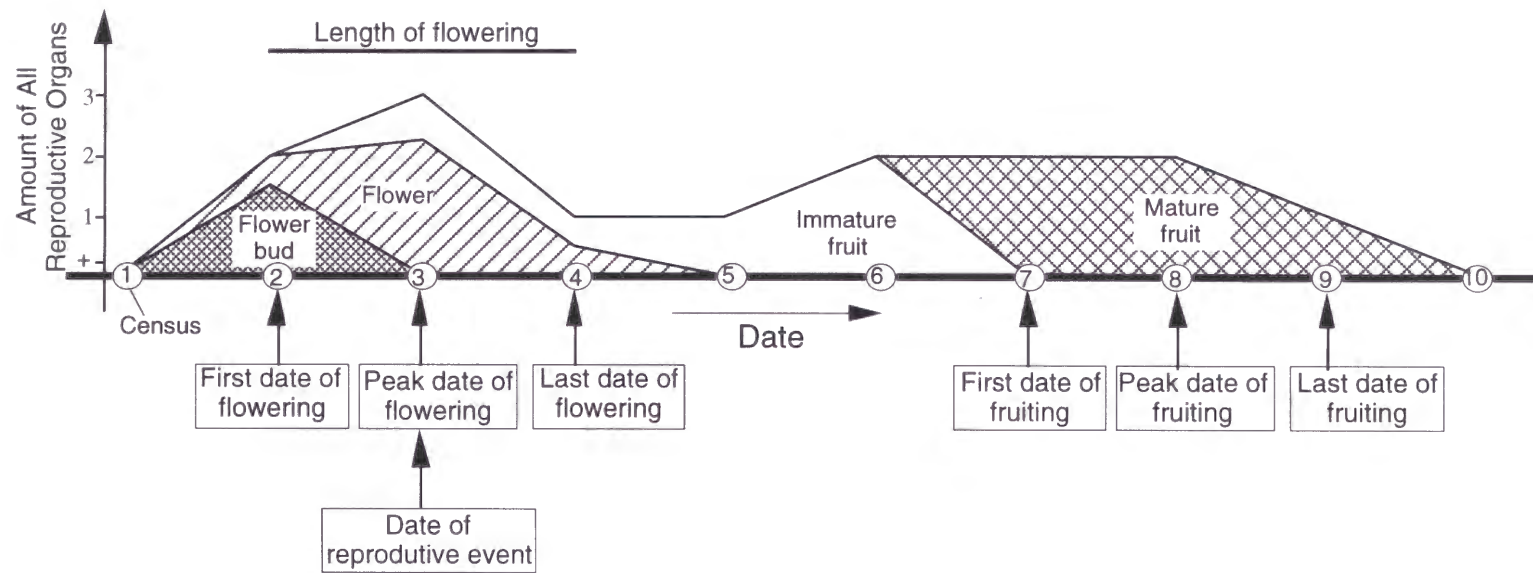


Fig. 3-1. A diagram of a reproductive event. The vertical axis shows the total amount of all reproductive organs described using four grades (+, 1, 2, 3) at each census with the proportions of flower buds, flowers and immature and mature fruits. For each reproductive event, the first, peak and last observation dates of flowering were recorded. The first and last date of flowering was the first (Census ② in the diagram) and last censuses (Census ④) in which flowers of the focal plant were observed. The peak date of flowering was determined as the date when the amount of reproductive organs was at its maximum in the flowering period (Census ③). In the same manner, the first (Census ⑦), peak (Census ⑧) and last observation dates (Census ⑨) of fruiting were recorded. The date of the reproductive event was represented by the peak of flowering (Census ③). Length of flowering period in each event was defined to be the number of days between the first (Census ②) and last dates (Census ④) of flowering. Magnitudes of the flowering, fruiting and whole reproductive event were determined to be the maximum grade of the quantity of reproductive organs through the period with flowers, mature fruits and the whole episode, respectively. In a case of reproductive event illustrated in the diagram, magnitude of flowering is grade 3 due to a record at Census ③ and magnitude of fruiting is grade 2 due to records at Censuses ⑦, ⑧).

length of flowering period was regarded as day “0”. The flowering length of each species was an average of the flowering length for all events of the species. Magnitudes of the flowering, fruiting and whole reproductive event were determined to be the maximum grade of the quantity of reproductive organs through the period with flowers, with mature fruits and the whole episode, respectively (Fig. 3-1). Events with magnitudes 1-3 were defined to be “effective” flowering, fruiting or reproduction in this paper.

Classification of flowering types

We defined the flowering types of 257 species based on phenological behaviors at the individual level. The flowering pattern of an individual was classified according to the timing and frequency of effective reproductive events over 43 months from June 1993 to December 1996. The period from March to December 1996, when reproducing individuals continuously exceeded 10% of all individuals under observation, was defined as a general flowering period (GFP). First, when all the reproductive events of an individual occurred during GFP, the individual was categorized as “general flowering type” independent of the number of the events during GFP. All other individuals were classified based on flowering frequency, following the definitions by Newstrom *et al.* (1994a). When the frequency was five or more during the 43 months, the individual was classified as “sub-annual”. When three or four, it was classified as “annual”, and when one or two, it was classified as “supra-annual”. When a species included individuals of more than one flowering types, I assigned the type of the majority as the flowering type of the species. If the two or more flowering types were equally common within a species, the flowering type of the species was determined in priority order from sub-annual to annual, supra-annual and general flowering. This is because less frequent reproduction may be caused by immaturity or unfavorable environmental

conditions, and because supra-annual species could be assigned to the general flowering category by mistake when flowering of some individuals coincided with a general flowering by chance.

We examined correlations between the proportions of general flowering species and the plant categories (life form types, pollination systems and fruit types) by χ^2 -tests. Species that were observed reproducing at least once during the 43 months and plant categories with more than 15 species were included in the analyses.

Statistical tests for reproductive events

Periodical concentration of all effective reproductive events within each three-month period from July 1993 to December 1996 was examined by Morisita's Index, I_d , an index of aggregation independent of sample size. This value will be near 1 in distributions that are essentially Poisson, > 1 in clumped samples, and < 1 in cases of regular, or seasonal reproduction (Morisita 1959). The χ^2 -test for goodness of fit was performed assuming that flowering events occurred at random throughout the 14 three-month periods (when the sample size ≥ 70) or 7 six-month periods (when $35 \leq \text{sample size} < 70$) from June 1993 so that the expected frequency in a unit period might be five or more (Sokal & Rohlf 1981). The analyses were also conducted by plant categories (taxonomic groups, life form types, pollination systems and fruit types). Correlations of the numbers of the effective reproductive events in every three-month period between flowering types were examined by Spearman's rank correlation test. In addition, interspecific aggregation of reproductive events was examined with the χ^2 -test for goodness of fit assuming that the numbers of reproductive species in three-month periods were distributed at random.

The averaged number of effective flowering events per month per individual of each flowering type during GFP and non-GFP was compared.

Individuals that reproduced at least once during the 43 months were included in the calculation. Fruit set (the proportions of effective flowering events resulting in effective fruiting to all the effective events) during non-GFP and GFP was compared by flowering types. Statistical significance of the difference between GFP and non-GFP was analyzed by Fisher's exact test (one-tailed).

The length of flowering period of each plant category was compared with that of the other species by the Wilcoxon two-sample test (two-tailed).

Result

Climatic conditions

Ashton *et al.* (1988) indicates that a drop of daily minimum temperature by 2 °C induce general flowering. In Lambir, daily minimum temperature was about 23 °C on the average (Fig. 3-2). Drops of daily minimum temperature < 21 °C at Miri Airport were observed three times during the study period: January-February 1993 for 6 days; January-February 1995 for 2 days; and December 1996 for 2 days. Drops at Lambir Hills National Park were also recorded three times while being recorded: August 1993 for 3 days; June 1994 for 1 day; and November 1995-February 1996 for 30 days (Fig. 3-2). The drop in December 1996 in Lambir was very strong, continuing intermittently from 14 November 1995 to 27 February 1996, with the lowest temperature 19.2 °C. At the same time, a drop was observed at Miri but was not as strong. The other drops were not coincident between the two sites except for a drop at Miri in December 1996, when data at Lambir were not collected. The correlation of minimum temperature between the two sites was statistically significant, though not strong ($P < 0.001$, $r^2 = 0.509$).

Disparity between Lambir and Miri Airport was found in rainfall data, too. In addition to differences in the total amount of rainfall between the two

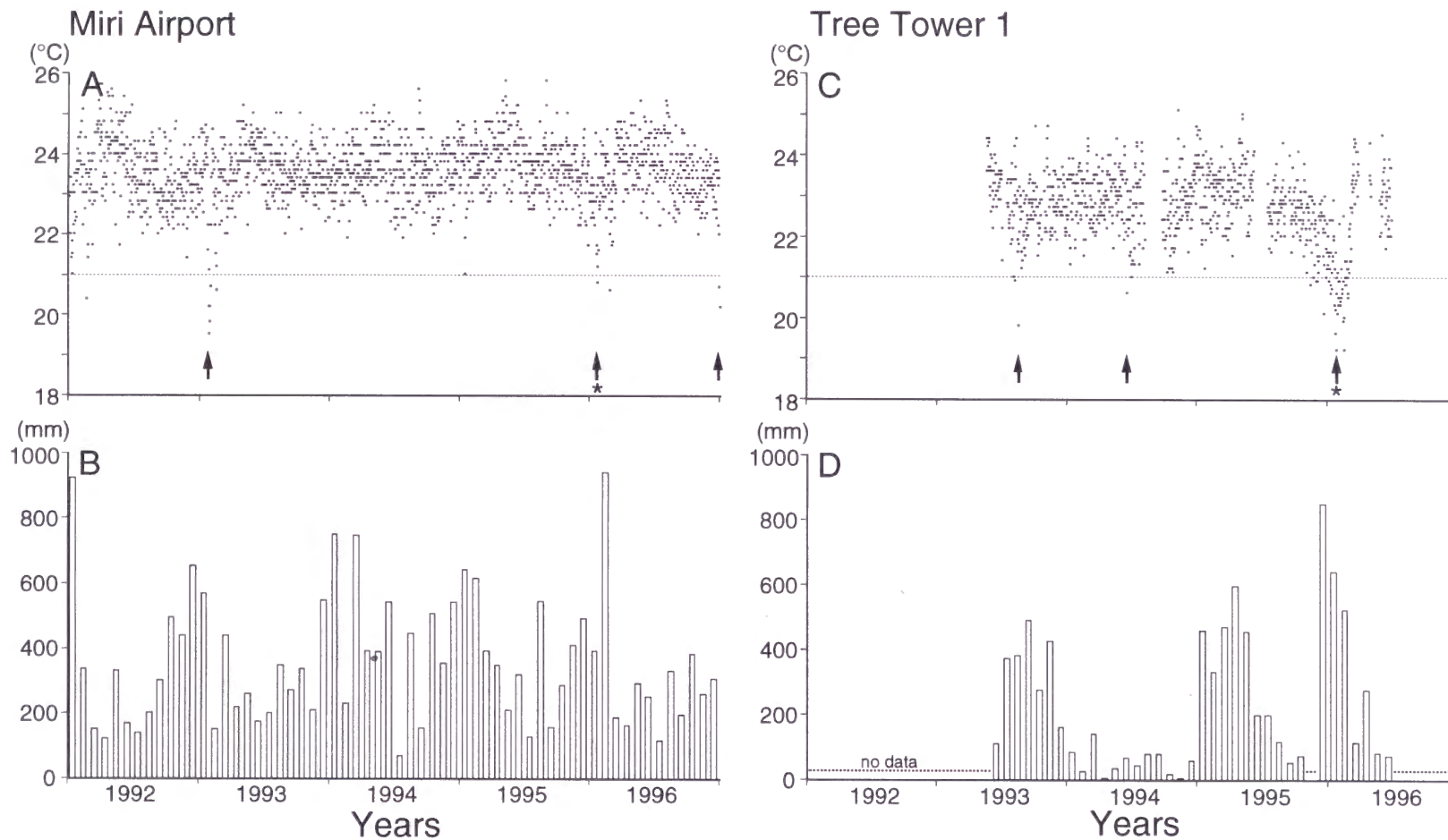


Fig. 3-2. The march of climate at Miri Airport, 20 km apart from Lambir National Park, and in the canopy at Lambir during the study, from 1992 to 1996. **A**, daily minimum temperature at Miri Airport; **B**, monthly rainfall (mm) at Miri Airport; **C**, daily minimum temperature in Lambir; **D**, Monthly rainfall (mm) at Lambir. In **A** and **C**, drops in minimum temperature lower than 21°C are indicated by arrows, among which a drop just before general flowering is indicated by an arrow with an asterisk.

sites, yearly and monthly fluctuation patterns were quite different. Lambir experienced drought in 1994, when average monthly precipitation was about a fifth of a normal year. However, the total precipitation at Miri Airport in 1994 was the highest in the five years, 1992-1996 (Fig. 3-2). Drops of temperature were rarely accompanied by drought except in 1994 at Lambir, when precipitation was small throughout the year.

Species, life form types, pollination systems and fruit types

The emergent layer was dominated by Dipterocarpaceae (78% of 48 spp., Table 3-2). In the lower layers, Anacardiaceae, Burseraceae, Euphorbiaceae and Myristicaceae were the most common families, but no one fairly dominated. Most lianas belonged to Leguminosae (20% out of 54 spp.), *Ficus* (16%, Moraceae) and Annonaceae (13%). All the observed lianas in *Ficus* were stranglers. Epiphytes included 14 spp. of Orchidaceae, 3 spp. of Loranthaceae and 2 spp. of Araceae.

The most common pollinators of the 305 plant species monitored were small social bees (25%) followed by beetles (23%), diverse insects (14%) and *Apis* bees (11%). In beetle pollination systems, dipterocarp and non-dipterocarp beetles accounted for about the same percentages, 11%. In the emergent layer, 58% and 17% of the 48 species were pollinated by dipterocarp beetles and *Apis*, respectively (Table 3-3, 4). In the lower layers, small social bees, diverse insects and non-dipterocarp beetle visitors predominated. Non-dipterocarp beetle pollination was found most often in Annonaceae and Myristicaceae (Table 3-4), which occupy lower layers or are lianas (Table 3-2). The plants pollinated by diverse insects and small social bees belonged to various families (Table 3-4). Most of the gap trees were pollinated by small social bees (7 out of 9 spp.). Long-distance pollinators such as mammals, birds, solitary bees and lepidopterans, played limited roles.

Table 3-2. Total number of species from several abundant families and genera by life form types. Numbers of individuals are shown in parentheses.

Family Genus	Life form type ^a						Total	%
	2	3	4	5	G	L	E	
Anacardiaceae		5 (5)	5 (9)		1 (4)			11 (18) 3.6 (3.1)
Annonaceae	1 (1)	3 (4)	1 (2)			7 (12)		12 (19) 3.9 (3.3)
Burseraceae		7 (11)	7 (11)	2 (3)				16 (25) 5.2 (4.3)
Dipterocarpaceae								
<i>Dipterocarpus</i>			1 (6)	5 (30)				6 (36) 2 (6.3)
<i>Dryobalanops</i>				2 (27)				2 (27) 0.7 (4.7)
<i>Shorea</i>			2 (7)	26 (98)				28 (105) 9.2 (18.2)
others		1 (3)	3 (6)	2 (2)				6 (11) 2 (1.9)
Euphorbiaceae	4 (8)	10 (19)	4 (10)		5 (19)	1 (2)		24 (58) 7.9 (10.1)
Leguminosae		3 (3)	6 (11)	5 (9)		11 (13)		25 (36) 8.2 (6.3)
Moraceae								
<i>Artocarpus</i>			8 (16)					8 (16) 2.6 (2.8)
<i>Ficus</i>						9 (13)	1 (1)	10 (14) 3.3 (2.4)
<i>Prainea</i>		1 (1)						1 (1) 0.3 (0.2)
Myristicaceae	1 (1)	10 (13)	4 (6)					15 (20) 4.9 (3.5)
Orchidaceae							12 (12)	12 (12) 3.9 (2.1)
Others	7 (7)	33 (40)	40 (64)	6 (13)	3 (3)	26 (34)	14 (17)	129 (178) 42.3 (30.9)
Total	13 (17)	73 (99)	81 (148)	48 (182)	9 (26)	54 (74)	27 (30)	305 (576) 100 (100)

^a 2, understory (2.5–12.5 m); 3, subcanopy (12.5–27.5 m); 4, canopy (27.5–42.5 m); 5, emergent (> 42.5 m); G, gap tree; L, liana; E, epiphyte.

Table 3-3. Total number of species by life form types, and pollination systems and fruit type.
Numbers of individuals are shown in parentheses.

	Life form type code ^a								
	2	3	4	5	G	L	E	Total	%
Pollination system (code)									
Mammal (M)		3 (5)	1 (1)		1 (1)			5 (7)	1.6 (1.2)
Bird (A)		1 (1)					3 (5)	4 (6)	1.3 (1.0)
<i>Apis</i> (BA)	1 (1)	6 (8)	12 (24)	8 (40)		5 (6)	1 (1)	33 (80)	10.8 (13.9)
Small social bee (BT)	4 (4)	27 (39)	25 (43)	5 (8)	7 (24)	7 (9)	2 (2)	77 (129)	25.2 (22.4)
Solitary bee (BO)	1 (1)	2 (2)	1 (6)			3 (7)		7 (16)	2.3 (2.8)
Fig wasp (F)						9 (14)	1 (1)	10 (14)	3.3 (2.4)
Beetle (C)	4 (4)	12 (18)	14 (31)	31 (116)		8 (16)		69 (185)	22.6 (32.1)
Dipterocarpaceae		1 (3)	6 (19)	28 (108)				35 (130)	11.5 (22.6)
Non-dipterocarp	4 (4)	11 (15)	8 (12)	3 (8)		8 (16)		34 (55)	11.1 (9.5)
Lepidopteran (L)		1 (1)		1 (15)				2 (16)	0.7 (2.8)
Diverse insects (DI)	2 (6)	16 (20)	20 (32)	1 (1)		4 (5)		43 (64)	14.1 (11.1)
Others (O)		3 (3)						3 (3)	1 (0.5)
Unknown (UN)	1 (1)	2 (2)	8 (11)	2 (2)	1 (1)	18 (18)	20 (21)	52 (56)	17 (9.7)
Fruit type (code)									
Animal (a)	9 (13)	39 (46)	36 (57)	2 (3)	5 (19)	16 (23)	6 (9)	113 (170)	37.0 (29.5)
large fruit (l)	4 (4)	24 (39)	37 (80)	43 (172)	2 (5)	12 (19)		122 (319)	40.0 (55.4)
Small fruit (s)		6 (10)	1 (1)	3 (7)	1 (1)	11 (17)	13 (13)	34 (48)	11.1 (8.3)
Unknown (un)		4 (4)	7 (10)		1 (1)	15 (15)	8 (8)	36 (39)	11.8 (6.8)
Total	13 (17)	73 (99)	81 (148)	48 (182)	9 (26)	54 (74)	27 (30)	305 (576)	100 (100)

^a 2, understory (2.5–12.5 m); 3, subcanopy (12.5–27.5 m); 4, canopy (27.5–42.5 m);

5, emergent (> 42.5 m); G, gap tree; L, liana; E, epiphyte.

Table 3-4. Total number of species in several families and genera by pollination systems and fruit types.

Numbers of individuals are shown in parentheses.

Family Genus	Pollination system code*											Fruit type*				All	%
	M	A	BA	BT	BO	F	C	L	DI	O	UN	a	l	s	un		
Anacardiaceae				11 (18)								3 (4)	8 (14)			11 (18)	3.6 (3.1)
Annonaceae							12 (19)					3 (4)	9 (15)			12 (19)	3.9 (3.3)
Burseraceae				13 (22)					2 (2)		1 (1)	8 (12)	5 (8)	1 (1)	2 (4)	16 (25)	5.2 (4.3)
Dipterocarpaceae																	
<i>Dipterocarpus</i>			2 (5)				3 (16)	1 (15)					6 (36)			6 (36)	2 (6.3)
<i>Dryobalanops</i>			2 (27)										2 (27)			2 (27)	0.7 (4.7)
<i>Shorea</i>							28 (105)						28 (105)			28 (105)	9.2 (18.2)
others			1 (1)				4 (9)				1 (1)		6 (11)			6 (11)	2 (1.9)
Euphorbiaceae			3 (5)	15 (41)					6 (12)			9 (27)	15 (31)			24 (58)	7.9 (10.1)
Leguminosae	2 (2)		12 (17)	3 (3)	2 (8)				1 (1)		5 (5)	5 (5)	8 (14)	7 (12)	5 (5)	25 (36)	8.2 (6.3)
Moraceae																	
<i>Artocarpus</i>									8 (16)			8 (16)				8 (16)	2.6 (2.8)
<i>Ficus</i>							10 (14)					10 (14)				10 (14)	3.3 (2.4)
<i>Prainea</i>									1 (1)				1 (1)			1 (1)	0.3 (0.2)
Myristicaceae							12 (17)			3 (3)		15 (20)				15 (20)	4.9 (3.5)
Orchidaceae			1 (1)								11 (11)			12 (12)		12 (12)	3.9 (2.1)
Others	3 (5)	4 (6)	12 (24)	35 (45)	5 (8)		10 (19)	1 (1)	28 (38)		34 (38)	52 (68)	34 (57)	15 (24)	28 (29)	129 (178)	42.3 (30.9)
Total species	5	4	33	77	7	10	69	2	43	3	52	113	122	35	35	305	100
Total individuals	(7)	(6)	(80)	(129)	(16)	(14)	(185)	(16)	(64)	(3)	(56)	(170)	(319)	(49)	(38)	(576)	100

* See Table 3-3.

Animal dispersal was frequent in subcanopy and canopy layers (Table 3-3). Prevalence of large fruit species in the emergent layer was due to dominance of Dipterocarpaceae (Table 3-4). Most small fruit species were legume lianas and epiphytic orchids (Tables 3-3, 4).

Flowering pattern at the community level

The final stage of general flowering in 1992 was detected as a high percentage of fruiting species and individuals in August 1992 by the censuses from TW and FF (Fig. 3-3). Observations from TW revealed that the percentage

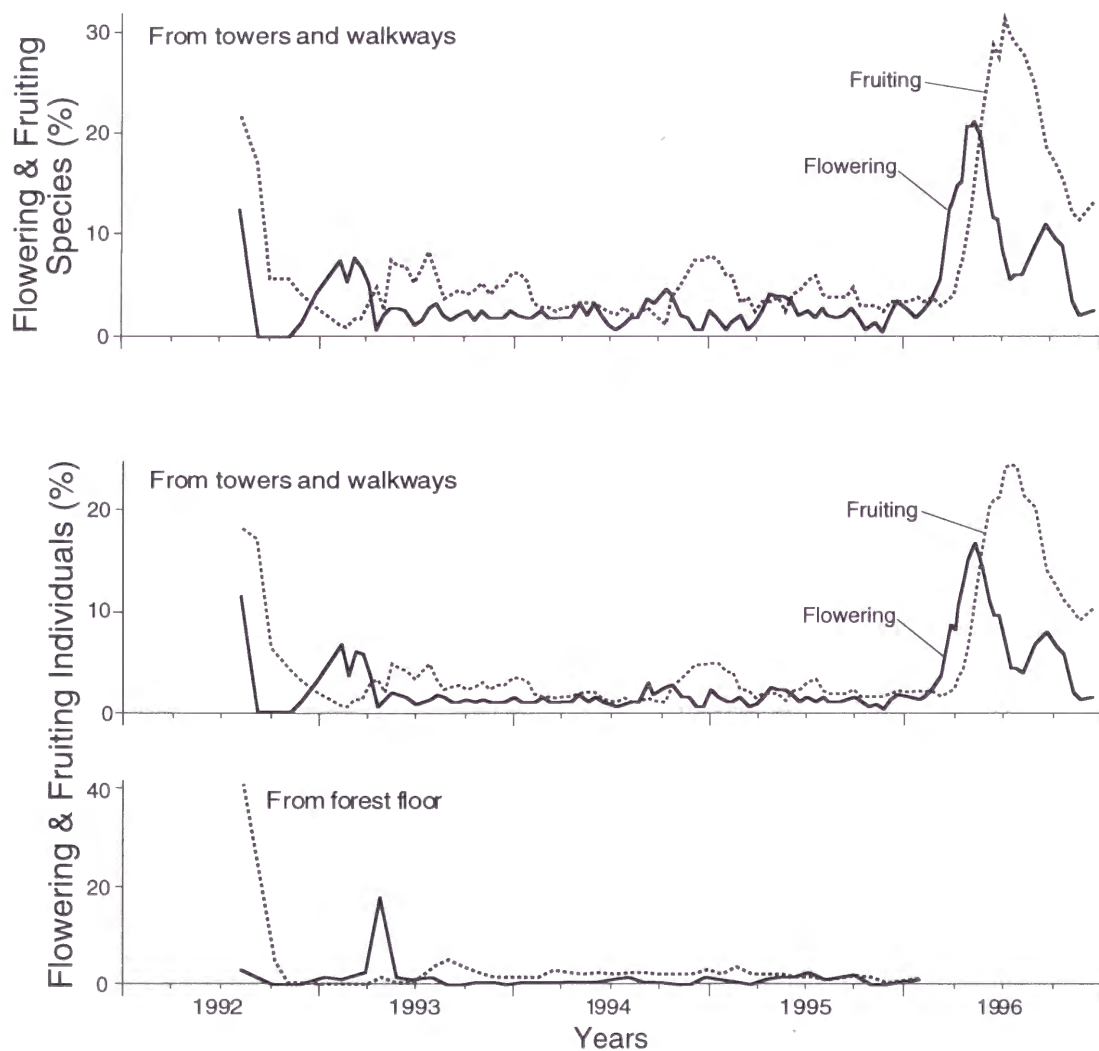


Fig. 3-3. Changes in the percentage of flowering and fruiting species and individuals observed from the forest floor (FF, 190 individuals) and tree towers and walkways (TW, 237 spp., 432 individuals).

of flowering individuals was low during non-GFP, usually less than 3.0% with a minor peak up to 6.7% in the first quarter of 1993. Minor increase of flowering individuals was recorded by the census from FF in April 1993 (Fig. 3-3). Among 33 individuals flowering at that time, 16 were Dipterocarpaceae including 2 spp. of *Dryobalanops*, *Dipterocarpus pachyphyllus* and 7 spp. of *Shorea*, though their intensities of reproduction were not recorded during this preliminary census period. The plants observed from TW did not show such a clear increase but small peaks were detected in February and March 1993. Reproductive events of 7 dipterocarp species with a magnitude “+” were recorded at that time.

The proportions of flowering species and individuals increased drastically in March 1996, and reached 16.9% and 21.1% respectively in May 1996. Another lower peak was observed in October 1996, half a year after the first peak, though a fruiting peak corresponding to the latter flowering peak did not appear in Fig. 3-3. It might be observed in 1997. I divided GFP into the first GFP, 1 May-24 July, and the second GFP, 25 July-31 December, corresponding to the two flowering peaks. During the first and second GFPs, 202 effective reproductive events of 129 spp. and 99 events of 69 spp. were recorded respectively.

General flowering started 1-2 months after a drop in minimum temperature observed at Lambir from December 1995 to February 1996, with the lowest temperature 19.2°C (Figs. 3-2, 3). Though two other minor drops to lower than 21 °C in August 1993 and July 1994 were observed, only the latter was followed by a small increase in the proportion of flowering individuals. Another minor flowering peak was observed in January-February 1994, but meteorological data were not collected at that time.

In total 664 reproductive events of 453 plants, including 527 effective reproductive events, were recorded during the 43 months (Table 3-5). More

Table 3-5. Temporal distribution of reproductive events recorded for 524 individuals monitored from TW for 43 months.

Year	Quarter ^a	Magnitude of reproductive event				Sum of 1-3	Total	No. of Species
		+	1	2	3			
	Jun-93	5		7		7	12	7
1993	3	22	1	14	1	16	38	14
	4	17	1	15	1	17	34	17
1994	1	12	1	10	1	12	24	11
	2	17	2	15	5	22	39	21
	3	12	1	14	6	21	33	18
	4	10	7	17	7	31	41	26
1995	1	4	3	7	9	19	23	14
	2	2	7	13	11	31	33	26
	3	6	7	7	7	21	27	20
	4	1	3	6	2	11	12	10
1996	1	2	12	15	17	44	46	35
	2	13	30	91	38	159	172	107
	3	7	24	28	19	71	78	53
	4	7	22	12	11	45	52	37
Total		137	121	271	135	527	664	

^a 1, Jan.-Mar.; 2, Apr.-June; 3, July-Sep.; 4, Oct.-Dec.

than a third (163 individuals) of the individuals reproduced only once, and about the same number of individuals (164) did not flower during the 43 months. Fifteen-seven percent out of the 527 effective events were concentrated during GFP especially in the three months from April to June 1996 (30%, 160 events). Both the reproductive events and the number of species reproducing in every three-month period were clumped significantly ($P < 0.001$, $I_d = 1.98$ for the events and $P < 0.001$, $I_d = 1.67$ for the number of species). At the species level, 72% of the 257 observed species reproduced at least once during the 43 months, and 61% flowered once or more during GFP.

Flowering types

The most abundant flowering type among the 257 spp. was general

flowering (35%), followed by supra-annual (19%), annual (13%), and sub-annual (5%) (Fig. 3-4, Table 3-6). Effective reproductive events were not observed for 72 spp. (28%) throughout the 43 months. Among general flowering species, the maximum number of reproductive events of an individual was recorded by *Bouea* sp. 1 (Anacardiaceae) and *Lophopetalum multinervium* (Celastraceae). A single individual of the two species reproduced three times and all of the reproductive events were concentrated in GFP. Apart from species that failed to flower, 53% of all the 185 species and 61% of the 135 tree species (except for epiphytes and lianas) flowered only once or twice during the 43 months.

Comparing among taxonomic groups, general flowering species dominated in *Dryobalanops*, *Dipterocarpus*, *Shorea* (all Dipterocarpaceae), Euphorbiaceae, Burseraceae and Orchidaceae (Fig. 3-4). The other dipterocarp species, including *Cotylelobium* (1 sp.), *Hopea* (1 sp.), *Parashorea* (1 sp.), and *Vatica* (3 spp.), were categorized into supra-annual type except for *V. badiifolia*. On the other hand, *Ficus* (Moraceae), exhibited the highest percentages of annual and sub-annual species, followed by Annonaceae and Myristicaceae. More than 44% of Anacardiaceae, Leguminosae, and *Artocarpus* (Moraceae) did not reproduce during the study period.

Results of χ^2 -tests for goodness of fit to random distribution of reproductive events strongly indicated that reproductive events of Dipterocarpaceae, *Shorea*, Euphorbiaceae and Leguminosae were significantly concentrated ($P < 0.001$, Table 3-6). The most strong aggregations were exhibited by *Artocarpus* ($I_{dr} = 9.3$), *Dipterocarpus* ($I_{dr} = 8.4$), *Dryobalanops* ($I_{dr} = 7.6$), and Burseraceae ($I_{dr} = 4.6$), though statistical significance of their aggregation could not be examined due to small sample size except in *Dryobalanops* ($P < 0.001$). On the other hand, the events of *Ficus* did not show

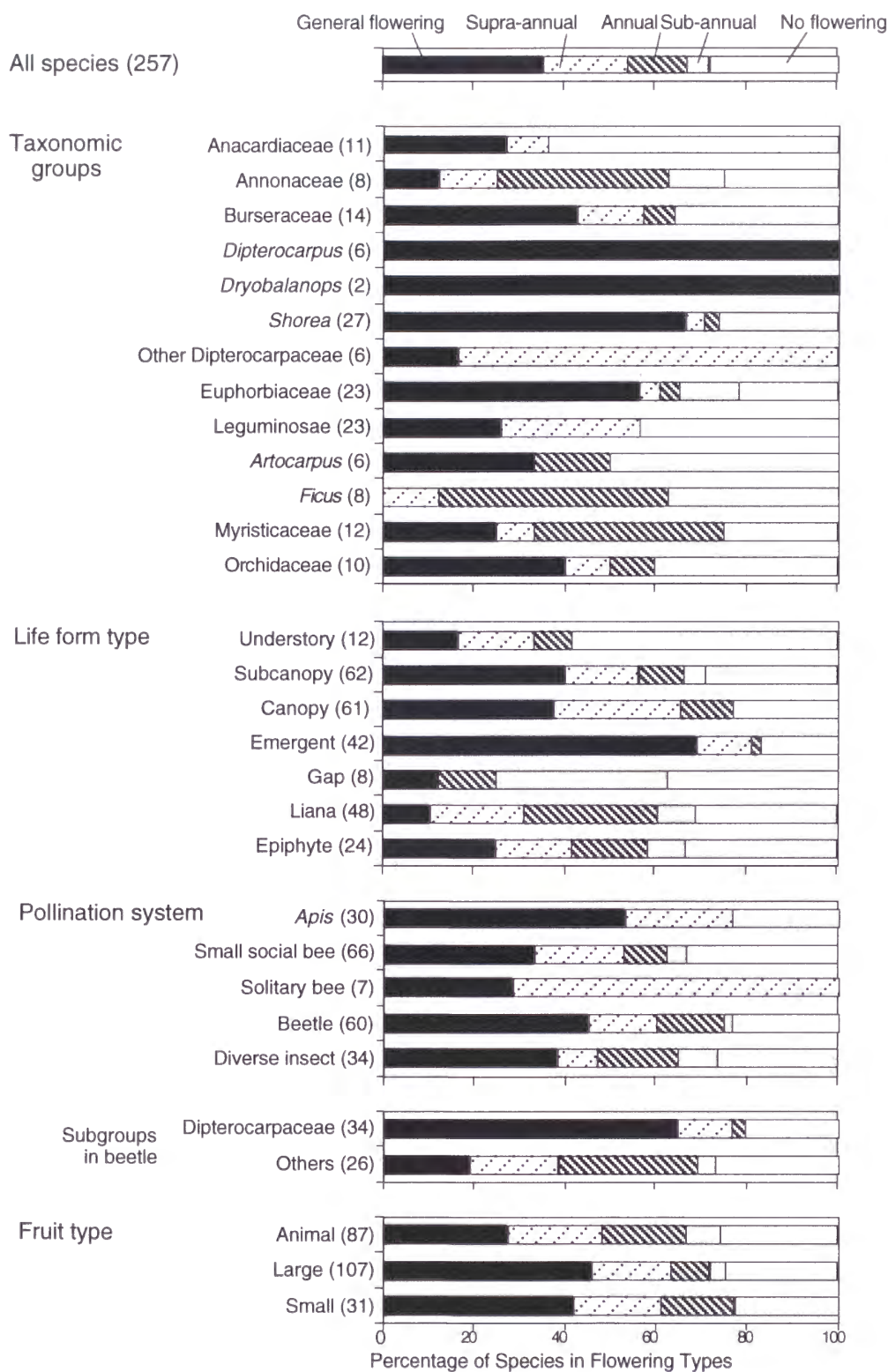


Fig. 3-4. The proportions of the four flowering types (sub-annual, annual, supra-annual and general flowering) and no flowering species among all species observed, taxonomic groups, life form types, pollination systems and fruit types. Pollination systems with less than 5 species are not included. Numbers of species included are shown in parentheses.

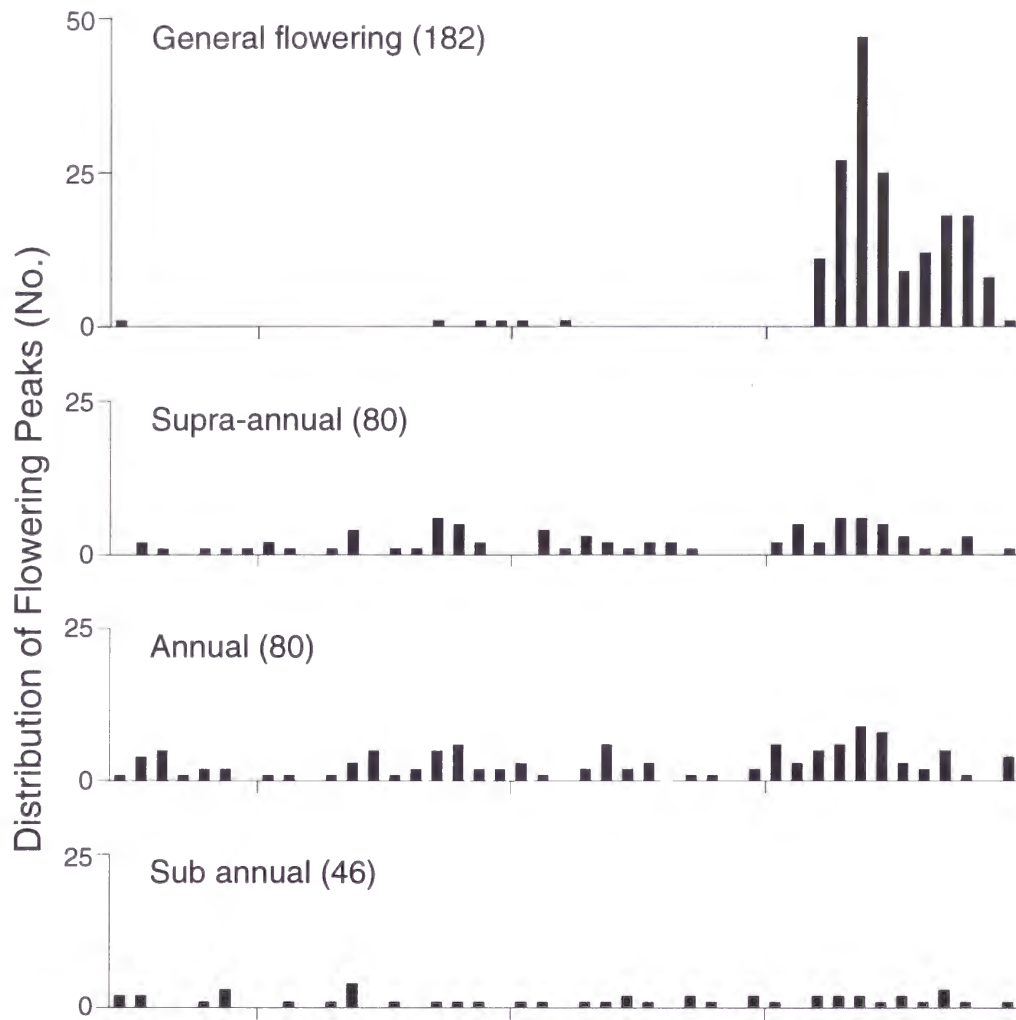


Fig. 3-5. Temporal distribution of effective flowering peaks in each month in the four flowering types. The numbers of the reproductive events included in the data are shown in parentheses.

aggregation ($I_d = 0.92$) (Table 3-6).

In the general flowering type, 97% of 182 effective flowering events were observed during GFP, and 54% from April to June (Fig. 3-5). Flowering events of general flowering type during non-GFP was also observed. They are due to flowering of small part of the population, while most individuals of the species did not flower during non-GFP. The same or different individuals of 27% of 91 general flowering species reproduced during both the first and second GFP.

Table 3-6. Number of species in main families and genera by flowering types.

Results of χ^2 -test for goodness of fit (one-sided) assuming that their flowering events occurred at random throughout the 14 three-month periods from July 1993 (when the sample size was 70 or more) or 7 six-month periods (when less than 70 and greater than 34) are shown.

Family	Flowering type					Total No. of species	No. of individuals ^a	No. of events	I_d	χ^2 -test for goodness of fit ^b
	No flowering	General flowering	Supra-annual	Annual	Sub-annual					
Anacardiaceae	7	3	1			11	16 (4)	6	3.73	-
Annonaceae	2	1	1	3	1	8	14 (8)	22	1.39	-
Burseraceae	5	6	2	1		14	20 (10)	14	4.62	-
Dipterocarpaceae										-
<i>Dipterocarpus</i>		6				6	33 (19)	22	8.42	-
<i>Dryobalanops</i>		2				2	16 (13)	15	7.60	-
<i>Shorea</i>	7	18	1	1		27	81 (45)	60	3.72	***
others		1	5			6	11 (9)	15	2.13	-
all	7	27	6	1		41	141 (86)	112	4.00	***
Euphorbiaceae	5	13	1	1	3	23	48 (37)	79	2.37	***
Leguminosae	10	6	7			23	30 (16)	18	2.84	-
Moraceae										
<i>Artocarpus</i>	3	2		1		6	8 (4)	6	9.33	-
<i>Ficus</i>			1	4	3	8	11 (9)	34	0.92	-
<i>Prainea</i>	1					1	1 (0)	0		-
all	4	2	1	5		15	20 (15)	41	1.06	-
Myristicaceae	3	3	1	5		12	17 (12)	30	1.51	-
Orchidaceae	4	4	1	1		10	10 (6)	9	2.72	-
Others	25	26	27	17	5	100	137 (97)	-	-	-
Total	72	91	48	34	12	257	453 (289)	520	2.15	***
%	28.0	35.4	18.7	13.2	4.7	100.0				

^a The numbers except for no flowering individuals are shown in parentheses.

^b ***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$; N.S., not significant; -, not examined because of small sample size.

The percentage of flowering events during GFP was much less in the other flowering types: 35% of 83 events of supra-annual; 37% of 117 events of annual; (23 spp. out of 48 spp.) reproduced during GFP nevertheless, and the average number of flowering events per month per individual was higher during GFP than during non-GFP (0.046 events/month-individual for GFP and 0.026 for non-GFP). The difference was larger in the annual flowering type (0.078 for GFP and 0.041 for non-GFP). The same tendency was also found in sub-annual species (0.125 for GFP and 0.078 for non-GFP).

Positive correlations in temporal distributions of flowering peaks were found between flowering types. The strongest correlation was detected between annual and supra-annual types (Spearman's correlation coefficient: $r_s = 0.68$, $P = 0.007$). The correlations between general flowering and supra-annual types, and general flowering and annual types were also significant ($r_s = 0.63$, $P = 0.017$ and $r_s = 0.57$, $P = 0.035$, respectively). No significant correlation was observed between sub-annual and the other flowering types.

Effective flowerings of general flowering, supra-annual and annual species during GFP yielded higher fruit set than during non-GFP (Table 3-7). The difference was the largest in the general flowering type. Fisher's exact tests

Table 3-7. Comparison of fruit set during GFP and non-GFP.

The proportions of effective flowerings resulted in effective fruitings during GFP and non-GFP are compared by flowering types. Results of Fisher's exact test (P , one-sided) are shown.

Flowering type	Non-GFP		GFP		P^a
	%	N	%	N	
General flowering	27.3	11	64.2	176	0.018*
Supra-annual	27.1	48	44.4	27	N.S.
Annual	30.3	76	50.0	42	0.028*
Subannual	19.4	31	13.3	15	N.S.

^a *, $P \leq 0.05$; N.S., not significant.

detected significant differences in general flowering ($P = 0.018$) and annual types ($P = 0.028$). On the other hand, fruit set was higher during non-GFP in sub-annual flowering species, but the difference was not significant.

Flowering patterns of life form types

The upper three forest strata life form types, the emergent, canopy and subcanopy, exhibited a drastic increase of flowering individuals in the 1996 GFP with two flowering peaks. During non-GFP, reproduction was scarcely observed in the emergent layer (Fig. 3-6). Half of the ten reproductive events observed in the understory type occurred during GFP. The sharp increase of flowering of gap type trees was due to synchronized flowering of *Macaranga hosei* (Euphorbiaceae). Epiphytes and lianas often flowered during both GFP and non-GFP, but the frequencies of flowering were generally higher during GFP.

The proportion of general flowering type was significantly different among life form types that included more than 15 species (subcanopy, canopy, emergent, liana, epiphyte) ($P < 0.001$). The proportion was the highest in the emergent type (69%) (Table 3-8, Fig. 3-4). In the canopy and subcanopy layers, the proportions were 38-40%. The proportions were much lower in the gap type trees, lianas and epiphytes (13%, 10% and 25%, respectively). More than half of the species (7 spp. in 12 spp.) in the understory did not flower. Temporal distribution of reproductive events of all the tree life form types examined exhibit aggregation in high degree ($P < 0.001$) (Table 3-8). In mature forest larger I_d was found in the higher strata ($I_d = 3.8, 2.6, 2.2$ and 1.6 for emergent, canopy, subcanopy and understory, respectively, Table 3-8). I_d of gap type trees (1.5) was smaller than non-gap trees. Epiphytes exhibited less but significant aggregation ($P = 0.029, I_d = 1.3$), while lianas did not.

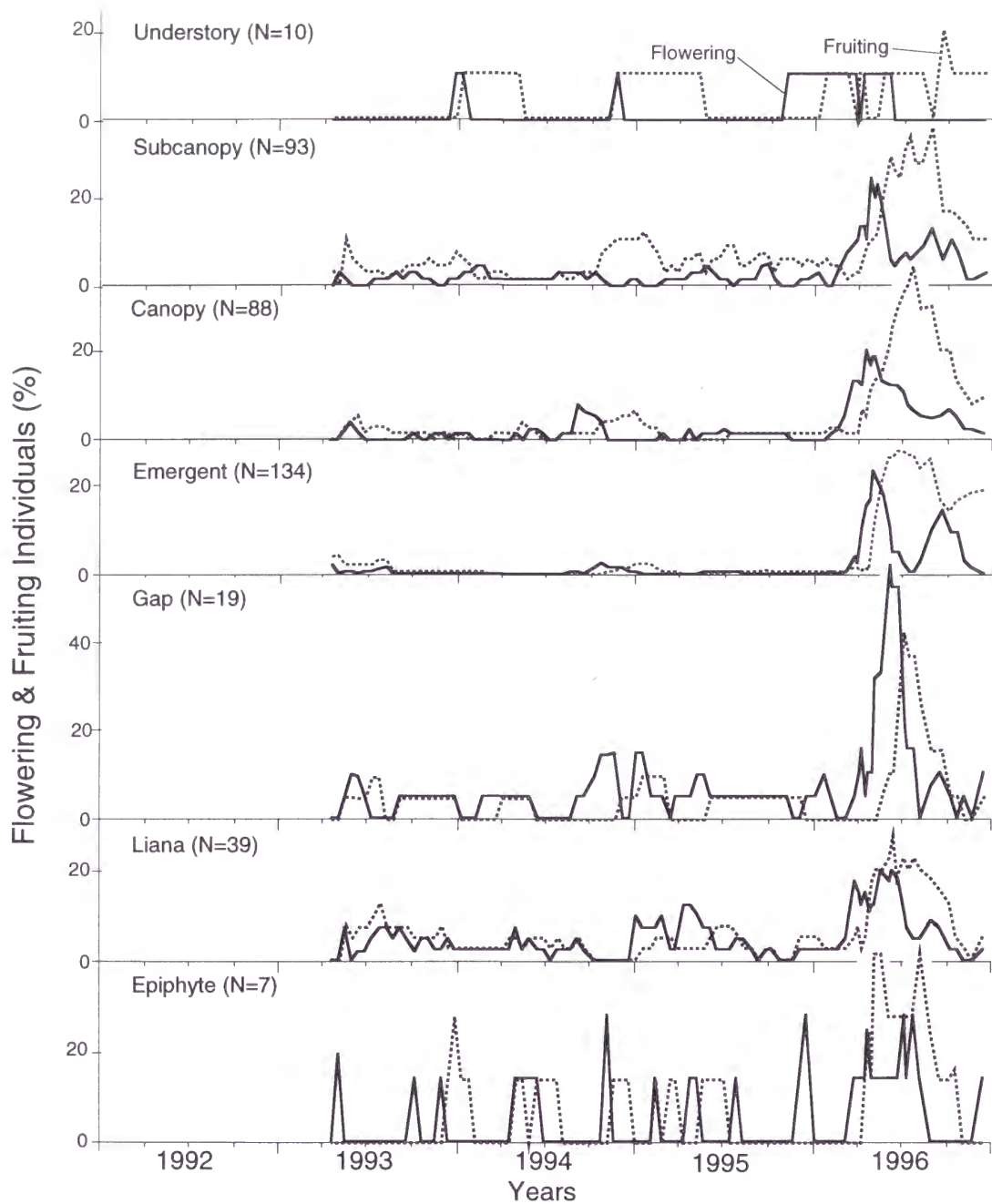


Fig. 3-6. Changes in percentage of flowering and fruiting individuals of seven plant life form types. Numbers of individuals observed are shown in parentheses.

Flowering patterns of pollination systems

The proportions of flowering individuals pollinated by *Apis* and dipterocarp beetles increased considerably during GFP, and was almost 0% during non-GFP (Fig. 3-7). On the other hand, a small proportion of individuals pollinated by small social bees, non-dipterocarp beetles, or diverse insects

Table 3-8. Number of species by flowering types and life form types.

Results of χ^2 -test for goodness of fit (one-sided) assuming that their flowering events occurred at random throughout the 14 three-month periods from June 1993 (when the sample size was 70 or more) or 7 six-month periods (when less than 70 and greater than 34) are shown.

Life form type (code)	Flowering type					Total No. of species	No. of individuals ^a	No. of events	I_d	χ^2 -test for goodness of fit ^b
	No flowering	General flowering	Supra- annual	Annual	Sub- annual					
Understory (2)	7	2	2	1		12	12 (5)	10	1.56	-
Subcanopy (3)	18	25	10	6	3	62	88 (55)	105	2.24	***
Canopy (4)	14	23	17	7		61	105 (68)	104	2.57	***
Emergent (5)	7	29	5	1		42	136 (86)	110	3.82	***
Gap (G)	3	1		1	3	8	20 (159)	48	1.49	***
Liana (L)	15	5	10	14	4	48	66 (42)	102	1.09	N.S.
Epiphyte (E)	8	6	4	4	2	24	26 (18)	41	1.28	*
Total	72	91	48	34	12	257	453 (289)	520	2.15	***
%	28.0	35.4	18.7	13.2	4.7	100.0				

^a The numbers except for no flowering individuals are shown in parentheses.

^b ***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$; N.S., not significant; -, not examined because of small sample size.

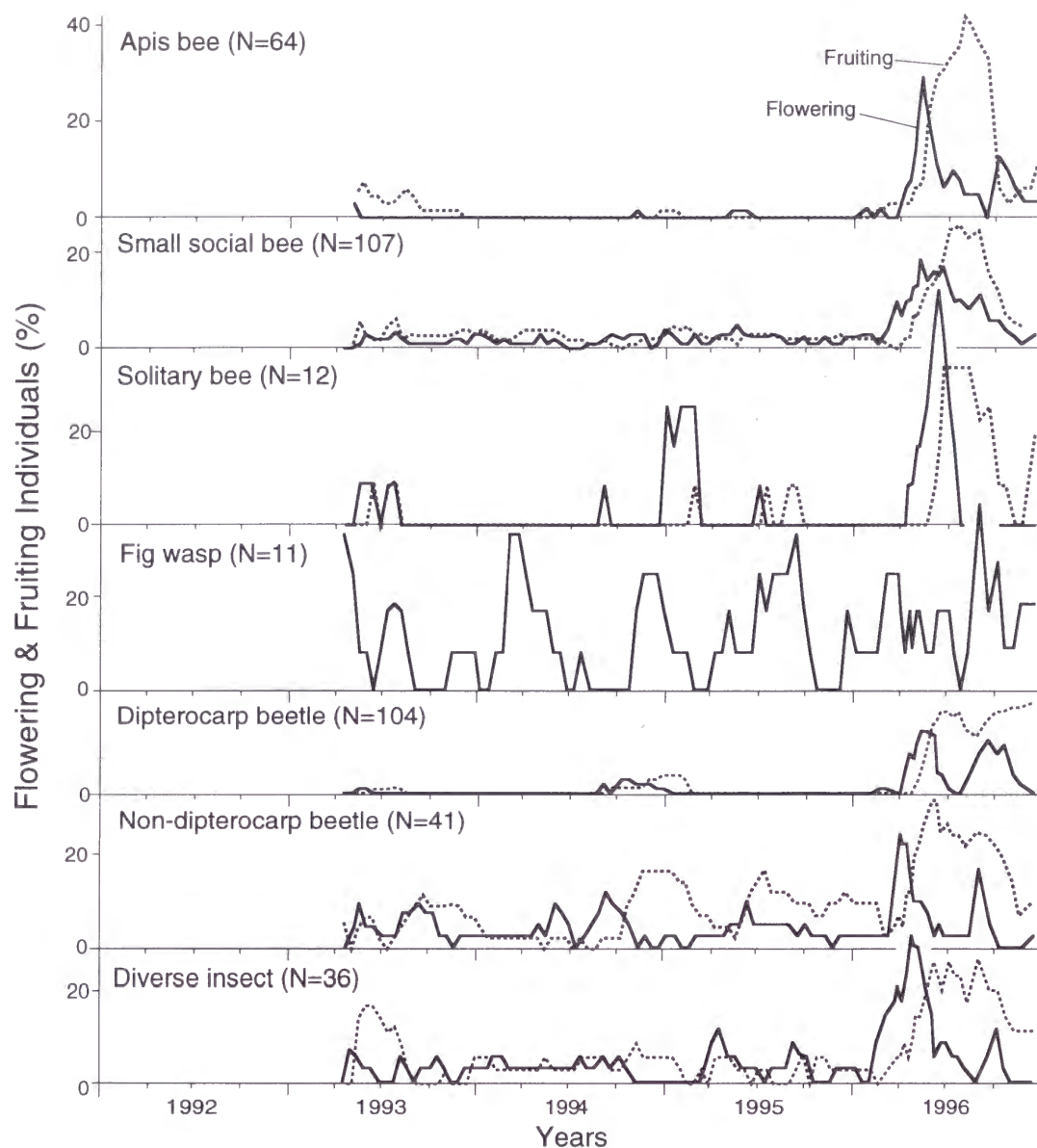


Fig. 3-7. Changes in percentage of flowering and fruiting individuals of seven pollination systems. Numbers of individuals observed are shown in parentheses. In the fig wasp pollination system, the percentage of individuals that have syconia is shown.

flowered one after another during non-GFP, so that they continuously flowered at the community level (Fig. 3-7). The proportion of flowering individuals in these plants became higher during GFP. Solitary-bee-pollinated plants exhibited sporadic reproduction (Fig. 3-7). The highest peak, in 1996, was due to flowering of *Sphenodesme triflora* (Verbenaceae) and *Callerya vasta* (Leguminosae); the second highest peak, in 1995, was flowering of *S. triflora*.

Ficus had unique flowering phenology and recorded a rather high percentage of reproducing plants continuously through the year. Their reproduction did not exhibit a significant difference from random distribution (Fig. 3-7).

The proportion of general flowering type was significantly different among pollination systems with more than 15 species (*Apis*, small social bee, non-dipterocarp beetle, dipterocarp beetle, diverse insect) ($P = 0.002$). A higher proportion of general flowering type was associated with *Apis* (53% out of 50 spp.) and beetles (45% out of 60 spp.) (Table 3-9, Fig. 3-4). In beetle systems, the percentage in Dipterocarpaceae (64% out of 34 spp.) was higher than that in other species (19% out of 26 spp.). Fig-wasp-pollinated *Ficus* (8 spp.) did not include any general flowering species. The other pollination systems had 25-38% of general flowering species. Bird-pollinated species included 3 spp. of Loranthaceae with frequent reproductive events and *Ardisia* (Myrsinaceae) of the general flowering type. Dominance of supra-annual types was only found in the solitary-bee-pollinated system. Two lepidopteran-pollinated species, *Dipterocarpus pachyphyllus* (Dipterocarpaceae) and *Barringtonia curranii* (Lecythidaceae) were the general flowering type. Reproductive events clumped significantly in *Apis*, small social bee, dipterocarp beetle and diverse insect pollination systems, but not in the non-dipterocarp beetle-pollinated species. Relatively large I_d was found in lepidopteran (5.0), *Apis* (4.7), and dipterocarp beetle (3.5) pollination systems (Table 3-9).

Flowering patterns of fruit types

All three fruit types showed a drastic increase of flowering and fruiting individuals during GFP (Fig. 3-8). Only large fruit species unambiguously showed the two-peaked flowering pattern. Changes in the proportion of individuals with mature fruits followed those of flowering about three months before. Sharpness of flowering and fruiting peaks, i.e. strength of temporal

Table 3-9. Number of species by flowering types, and pollination systems and fruit types.

Results of χ^2 -test for goodness of fit (one-sided) assuming that their flowering events occurred at random throughout the 14 three-month periods from July 1993 (when the sample size was 70 or more) or 7 six-month periods (when less than 70 and greater than 34) are shown.

	Flowering type					Total No. of species	No. of individuals ^a	No. of events	I_d	χ^2 -test for goodness of fit ^b
	No flowering	General flowering	Supra- annual	Annual	Sub- annual					
Pollination system (code)										
Mammal (M)	1	1	1			3	5 (2)	2	0.00	-
Bird (A)		1		2	1	4	5 (5)	18	0.92	-
<i>Apis</i> (BA)	7	16	7			30	63 (42)	48	4.69	***
Small social bee (BT)	22	22	13	6	3	66	106 (67)	133	1.90	***
Solitary bee (BO)		2	5			7	13 (12)	17	2.26	-
Fig wasp (F)			1	4	3	8	11 (11)	34	0.92	-
Beetle (C)	14	27	9	9	1	60	148 (88)	143	2.23	***
Dipterocarpaceae	7	22	4	1		34	105 (60)	81	3.46	***
Others	7	5	5	8	1	26	43 (28)	62	1.47	N.S.
Lepidopteran (L)		2				2	14 (8)	10	4.98	-
Diverse insect (DI)	9	13	3	6	3	34	44 (31)	64	2.10	***
Others (O)		1				1	1 (1)	1	-	-
Unknown (UN)	19	5	9	8	1	42	43 (24)	50	-	-
Fruit type (code)										
Animal (a)	22	24	18	16	7	87	121 (88)	201	1.46	***
Gravity (g)	26	49	19	9	4	107	254 (153)	235	2.62	***
Wind (w)	8	13	6	5	0	31	45 (32)	49	2.11	***
Unknown (un)	16	5	5	4	1	32	35 (18)	37	-	-
Total	72	91	48	34	12	257	453 (289)	520	2.15	***
%	28.0	35.4	18.7	13.2	4.7	100.0				

^a The numbers except for no flowering individuals are shown in parentheses.

^b ***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$; N.S., not significant; -, not examined because of small sample size.

aggregation of flowering and fruiting, differed little among the three fruit types. During non-GFP, large fruit species exhibited less reproduction than the other species.

The proportion of general flowering type was significantly different among the fruit types ($P = 0.017$), though the differences were smaller than those among the life form types and pollination systems. The general flowering type was less common in animal dispersed species, and was equally common in small and large fruit type (Fig. 3-4). Distribution of flowering events was significantly aggregated in all fruit types. The largest I_d , in the large fruit type, was mainly due to their having few reproductive events during non-GFP (Table 3-9).

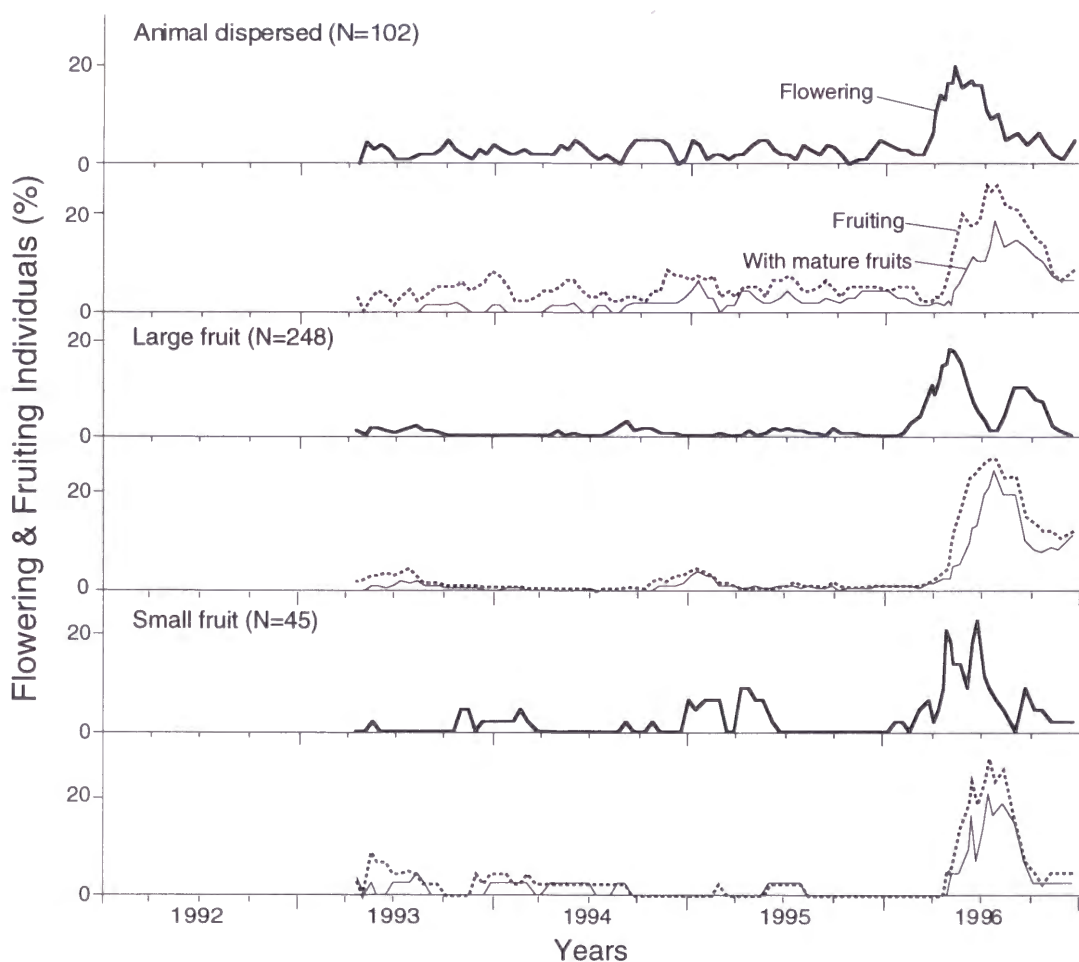


Fig. 3-8. Changes in percentage of flowering and fruiting individuals of three fruit types. Numbers of individuals observed are shown in parentheses.

Flowering patterns at population level

Flowering and fruiting patterns of three species, classified in different flowering types, were examined at the population level (Fig. 3-9). Most of them showed synchronized flowering among individuals irrespective of flowering types. An emergent species of *Dryobalanops aromatica* (Dipterocarpaceae) was a general flowering species with two flowering peaks during GFP (Fig. 3-9).

Among 11 individuals, 7 and 3 individuals flowered in the first and second GFP, respectively. Only one individual reproduced in both periods.

Sphenodesme triflora (Verbenaceae), a subcanopy species, was categorized as the supra-annual type. All 4 individuals under observation flowered at the beginning of 1995, and three reproduced again during GFP. A gap tree,

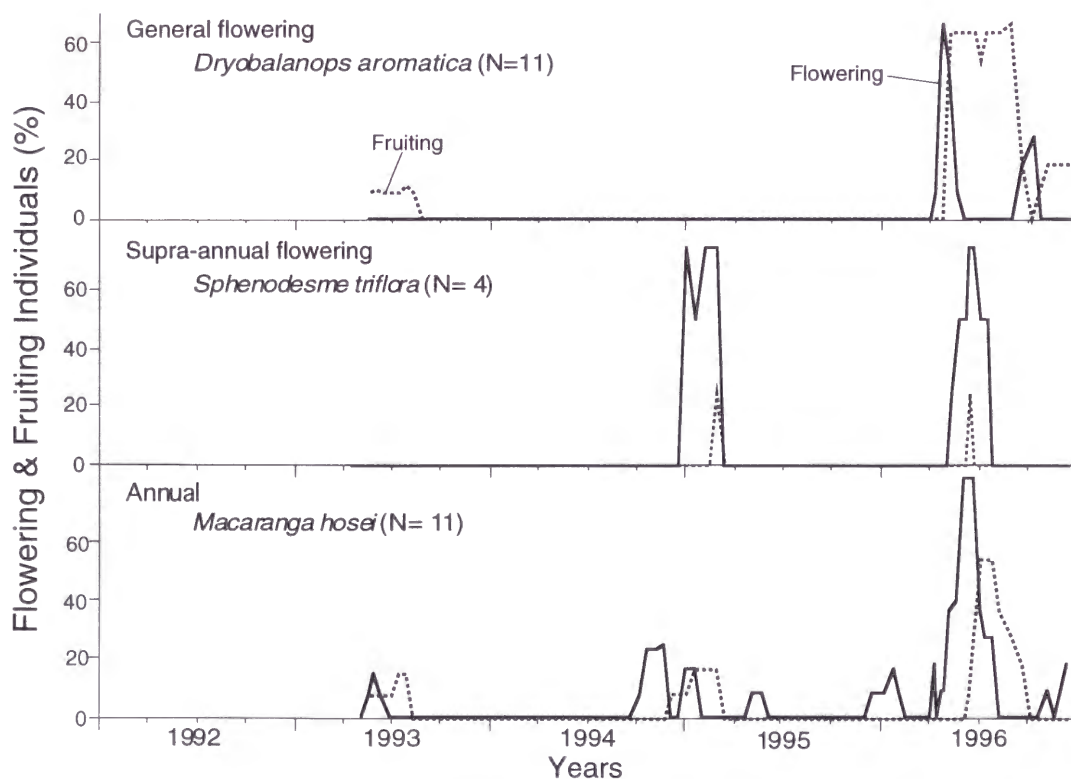


Fig. 3-9. Changes in percentage of flowering and fruiting individuals of three species (*Dryobalanops aromatica*, Dipterocarpaceae; *Sphenodesme triflora*, Verbenaceae; *Macaranga hosei*, Euphorbiaceae) of different flowering types. Numbers of individuals observed are shown in parentheses.

Macaranga hosei (Euphorbiaceae), reproduced rather frequently and showed annual flowering. Flowering was synchronized among individuals but the flowering intervals were irregular (Fig. 3-9). Only a few trees of the species participated in each flowering event during non-GFP, while up to 9 out of 11 individuals flowered at the same time and all individuals flowered 1-3 times during GFP. Other supra-annual and annual species with more than three reproductive individuals were showed flowering patterns similar to those of that were similar to those of *S. triflora* and *M. hosei*. Annual species, *Shorea beccariana* (Dipterocarpaceae) and *Knema latifolia* (Myristicaceae), flowered more frequently during GFP than non-GFP. *Vatica* aff. *parvifolia* (Dipterocarpaceae) flowered once during GFP and once during non-GFP. *Omphalea bracteolata* (Euphorbiaceae) is a sub-annual flowering liana. Of two individuals monitored, only one individual reproduced, seven times, and intra-specific synchronization could not be examined (Fig. 3-9).

Length of flowering period

The four flowering types, nine taxonomic groups, seven life form types 11 pollination systems, and three fruit types did not show significant difference in length of flowering period from the rest of the species, although there is considerable variation (Fig. 3-10). The species flowering longer than 120 days were a liana, *Artabotrys venustus* (Annonaceae), a canopy tree, *Coelostgia griffithii* (Bombacaceae) and a subcanopy tree, *Vernonia arborea* (Asteraceae). The former two species were pollinated by beetles, and the latter by *Apis*. For individuals of *A. venustus* and *Callicarpa pentandra* (Verbenaceae) flowerings were observed in more than half of all the observations.

Discussion

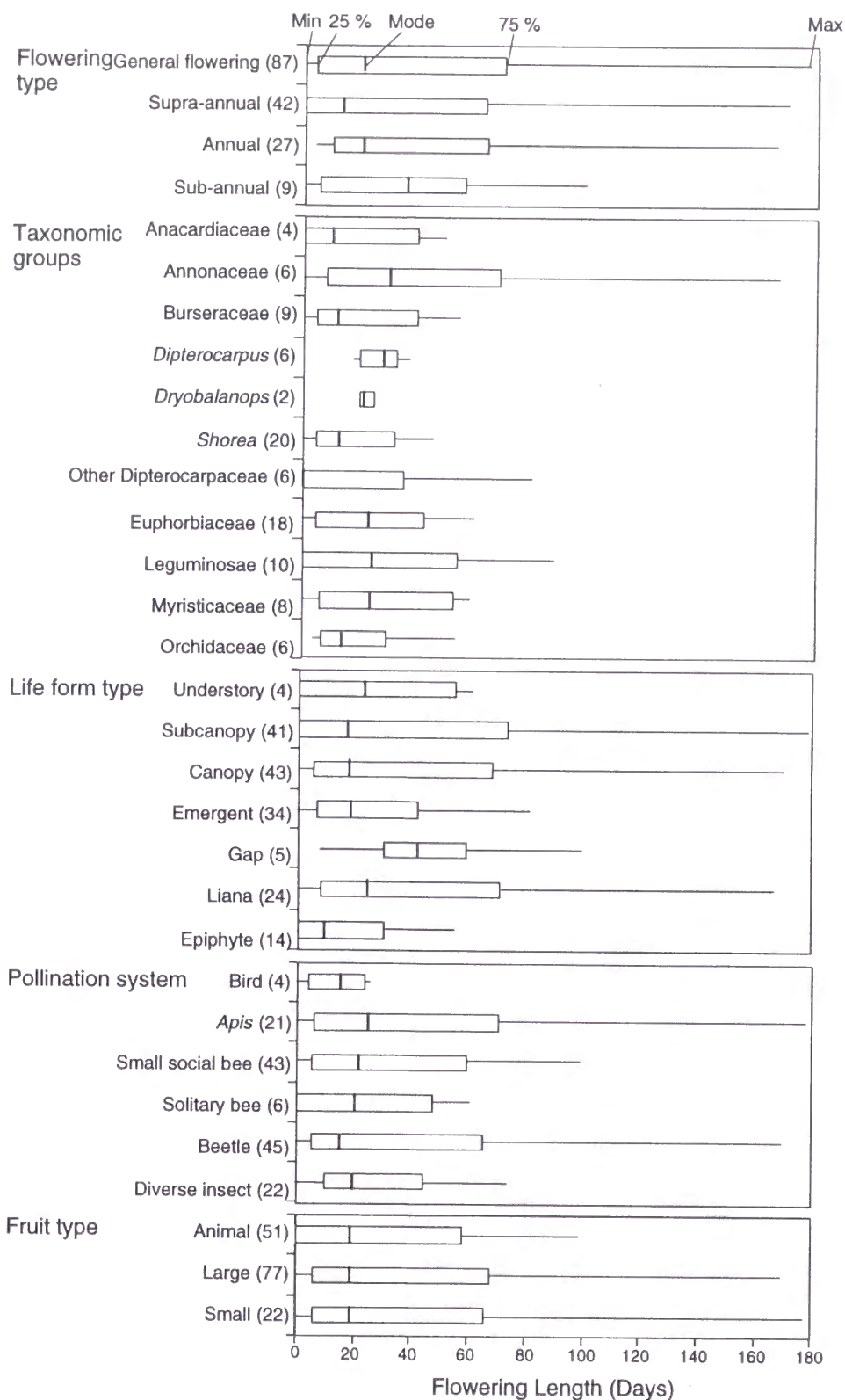


Fig. 3-10. Distribution of length of flowering periods by flowering types, taxonomic groups, life form types, pollination systems and fruit types. In the graphs, modes, points of 25% and 75% of the distributions, and maximum and minimum length are shown. The numbers of the species included are shown in parentheses.

General patterns

In this study, one cycle of the general flowering phenomenon was recorded at the community level in the lowland mixed dipterocarp forest in Lambir. The proportions of flowering species and individuals among the observed plants were quite low less than 5 % from 1992 to 1995, while the proportion drastically increased up to 17 % and 21 %, respectively. Thus, supra annual seasonality was found in plant reproductive phenology in the forest.

Aggregation of flowering events was found both at the population level and at the community level. The observed patterns suggested that most plants flowered with strong intraspecific synchronization and that flowering patterns observed at the individual level were the same as those at the population level, although flowering patterns at the population level were only examined in several species because of the low densities of conspecific adult trees at Lambir. Besides, reproductive events were strongly aggregated among species. Even supra-annual or annual species reproduced more actively during GFP, and significant positive correlations in flowering frequency were detected among supra-annual, annual and general flowering types, especially between supra-annual and annual flowering types.

One of the possible causes of the correlations is that the plants may adopt a common environmental variable as a trigger of flower induction. Differences in their flowering frequencies may reflect variation of the threshold values among species. Supra-annual and annual species reproduced more frequently during GFP than during non-GFP. They flowered in GFP not because their flowering is induced by a different environmental cue from that of general flowering species, but because they have higher thresholds to induce flowering than that of general flowering species. On the other hand, small part of individuals classified as general flowering type also flowered during non-GFP. It accord with a study by Yap & Chan (1990), which reports existence of an

intermediate intensity of flowering in addition to gregarious flowering in several species of *Shorea* (Dipterocarpaceae), representatives of general flowering species. Therefore, general flowering species and others may be continuous and differ quantitatively rather than qualitatively.

Relationship between flowering patterns and plant characters

In spite of strong correlations among plant taxonomic groups, life form types, pollination and fruit types, I analyzed data without using multivariate or phylogenetic analyses. It is because the purpose of the statistical tests conducted here is to examine whether observed patterns deviate from chance.

When the temporal distribution of flowering was examined by the plant categories (taxonomic groups, life form types and pollination and fruit types) using I_d and χ^2 -tests, most showed statistically significant aggregation. In addition, general flowering species were found in various plant categories. The general flowering phenomenon, which is a drastic increase of reproductive activity during a restricted period which occurs every 2-10 years with low activity in intervening periods, is fairly prevalent in many plant groups. However, comparison of flowering patterns, I_d and the proportion of general flowering species revealed that there were significant differences in flowering patterns among the plant categories.

Concentration of flowering events during GFP was more obvious in species found in the upper strata of the forest. Annual and sub-annual species were more frequent in the subcanopy and canopy than in the emergent layer. In the understory, more than half of the observed species were not observed flowering. Temporal aggregations of flowering events in gap trees, epiphytes and lianas were weaker than in trees in mature parts of the forest.

A theoretical model (Momose *et al.* 1998a) addresses differences in flowering intervals among the plants belonging to different forest strata. The

model assumes that flowering intervals of the trees maximize visits by pollinators, including opportunist and social bees, throughout their lifetimes. The model also assumes that larger displays attract more opportunist pollinators per flower. By contrast, the number of the social pollinators per flower is constant irrespective of display size, and social foragers recruit colony members once a display exceeds a minimum size.

When productivity is an increasing function and mortality is a decreasing function of plant size, trees in the highest canopy layers enjoy high productivity and low mortality. Their low mortality enables them to wait long intervals between flowering, and their high productivity allows them displays huge enough to attract many opportunist pollinators. On the other hand, the canopy or subcanopy trees cannot wait as long between reproductive episodes because of higher mortality. For these trees it is optimal to reproduce frequently with smaller display to attract social bees. The higher proportion of social-bee pollinated plants in the canopy and subcanopy trees than in emergent trees supports this idea.

Considerable differences among pollination systems in flowering patterns were found. The differences may be related to characteristics of their pollinators. One of the pollination systems working during GFP is reported in the next chapter, and general relationship between pollination systems and flowering pattern is discussed in Chapter 5.

General patterns of flowering and fruiting were not very different among the three fruit types, while animal dispersed species reproduced during non-GFP more frequently than the others. Differences in fruiting pattern among plants with different fruit dispersal modes have been reported in other studies. In a semideciduous forest in southeastern Brazil, wind-dispersed climbers showed a clear fruiting peak in the dry season, while animal-dispersed climbers had fruits throughout the year (Morellato & Leitão-Filho 1996). They suggested

that competition for fruit dispersers might have caused the pattern. It may not be difficult for many plants to delay fruit maturation until the optimal season for fruit dispersal (Wheelwright 1985).

Chapter 4. Pollination system in a general flowering period

Introduction

Although what pollination systems are adopted by plants which flower only in general flowering periods (GFP) and how the pollinators can maintain their populations is quite interesting and important problems (Ashton 1988; Appanah 1990), there are only a few studies on pollination systems in GFP. One of important pollinators is giant honey bees, which migrate into the forest when general flowering starts, and leave the forest after general flowering finished (Nagamitsu 1998, Momose *et al.* 1998b). Giant honey bees pollinate various plants including two species of *Dryobalanops*, two of most abundant dipterocarp species in the forest (Momose *et al.* 1998b).

Thrips are thought to be other important pollinators. According to studies from Pasoh Forest Reserve, Peninsular Malaysia (Chan & Appanah 1980; Appanah & Chan 1981), all six species of *Shorea* sect. *Mutica* in the forest including *S. parvifolia* Dyer were exclusively visited and pollinated by thrips in GFP. Appanah and his colleague noted that the short generation time and high reproductive rate of thrips permit a quick response of thrips to an abrupt increase of flowers at the beginning of the general flowering and that thrips provide sufficient pollination service for multiple species of *Shorea*.

Among the nine species of sect. *Mutica* monitored in the phenology censuses (Chapter 3), four species flowered in GFP. Unexpectedly, however, beetles were found to be the predominant flower visitors of all nine species of *Shorea* sect. *Mutica*, and also other sections under observation in emergent and canopy layers of the forest (Momose *et al.* 1998b).

This chapter presents field observations and experiments on the breeding and pollination system of an emergent tree species, *Shorea parvifolia*, a

member of sect. *Mutica*. The canopy observation system allowed continuous observation of pollination and reproductive processes, and manipulation of experiments on tree crowns over 60 m above the ground. In addition to flower visitation frequency and the amount of body pollen loads, the ability of flower visitors to effect fruit set was examined by experiments in which potential pollinators were introduced to bagged flowering inflorescences. Based on the results of observation and experiments, I examined whether thrips is dominant and exclusive pollinators of *S. parvifolia* as observed in Peninsular Malaysia, and discuss how pollinators of *S. parvifolia*, which flowers only in GFP, maintain their populations.

Materials and methods

Plant species

The genus *Shorea* (Dipterocarpaceae) is the dominant emergent tree genus of the lowland forest of West Malesia, with 163 species throughout Malesia (Ashton 1982; Ashton *et al.* 1988) and 65 species in Lambir (P. S. Ashton, personal communication). *Shorea parvifolia* is a member of sect. *Mutica* with 27 species in Malesia and 14 species in Lambir, and is one of the constituents of the emergent layer. In Canopy Biology Plot (Chapter 2), eight trees of *S. parvifolia* with > 40 cm dbh (diameter at breast height) were found. Nine individuals of *S. parvifolia* was part of focal plants in monitoring of phenology in Chapter 3, but three of them died before 1996.

Pollination of three individuals of *S. parvifolia* was studied during 14-28 May 1996. Two trees in Canopy Biology Plot, trees #225 (132 cm dbh, height 60 m) and #229 (44 cm dbh, height 35 m) (Table 4-1), were accessed by the canopy observation system. In addition, a crown of one other emergent tree near the headquarters of the national park (tree #1001) was accessed by aluminum ladders.

Table 4-1. Individuals of *Shorea parvifolia* observed from tree towers and walkways with developmental stage (DS). Magnitudes of flowering and fruiting in the two flowering periods in 1996 are shown using following grades: –, (flowers/fruits) absent; +, few, scattered, or covering only a small part of the crown; 1, covering less than half of the crown; 2, abundant but not over the whole crown; 3, covering the whole crown. No flowering with a grade '+' was observed. Flowering period is shown in parentheses.

Tree	DS ^a	No. of reproductive events during Aug1993–Dec1996	30 April–22 June		19 Sep–7 Nov	
			Flowering grade (flowering period)	Fruiting grade	Flowering grade (flowering period)	Fruiting grade
#233	III	0	–	–	–	–
#235	III	0	–	–	–	–
#228	IV	1	–	–	3 (15 day: 8 Oct–22 Oct)	2
#229	IV	1	3 (27 day: 11 May–6 June)	2	–	–
#225	V	2	3 (42 day: 30 April–10 June)	2	1 (19 day: 10 Oct–28 Oct)	–
#231	V	2	3 (33 day: 21 May–22 June)	2	3 (49 day: 19 Sep–7 Nov)	2
#161	V	died in Aug 1993	–	–	–	–
#230	V	died in Jan 1996	–	–	–	–
#232	V	died in Sep 1994	–	–	–	–

^aIII: subcanopy trees, 12.5–27.5 m; IV: canopy trees, 27.5–42.5 m; V: emergent trees > 42.5 m.

Collection of flower visitors and pollen on stigma

Flower visitors were collected by net-sweeping or by flower collection. In net-sweeping, a branch with about 200 open flowers were put into an insect net and quickly shook insects into the nets. The insects were transferred into a sealable plastic bag. The procedure were repeated five times on different branches at each collection time. The numbers of beetles and thrips per flower were calculated from eight samples taken on 13-15 May 1996 (18:00 and 22:00 on 13 May; 03:00, 10:00, 17:30 and 22:30 on 14 May; 02:30 and 06:30 on 15 May) on tree #225. Variation in flower visitors among the trees was examined using additional samples collected at 17:00 on 19 May on trees #225 and #229, and at 10:00 on 16 May and 17:00 on 20 May on tree #1001. The insects were brought to the laboratory within an hour and killed in a refrigerator. They were then pinned or fixed in alcohol and labeled.

Flower visitors that hid inside the corollas and could not be collected by net-sweeping were collected by flower collection. For flower collection, inflorescences with 46-124 flowers on tree #225 were cut off inside a sealable plastic bag. The plastic bags were brought to the laboratory and flower visitors in each of the corollas were counted under a binocular microscope, including flower visitors fallen from the corollas in the bag. The insects were preserved for identification in vials filled with 50% alcohol, except for thrips, which were kept in vials with glycerin-alcohol. Two bags were sampled at each collection time at 6-hour intervals on 16 May on tree #225.

The eight net-sweeping samples on 13-15 May and the four flower-collection samples on 16 May were used to examine changes in the densities of beetles and thrips in the crown in a day. The numbers of insects per flower during four 6-hour periods were calculated by summing the averaged number

of insects per flower collected by net-sweeping during the period and that by flower sampling. Standard errors for thrips numbers were calculated using flower collection samples, and those for beetle numbers were calculated using net-sweeping samples. Then I adjusted the standard errors to the total means of both samples. The standard error for beetles at 12:00 were not computed because only one net-sweeping sample was available.

Some of the beetles and thrips from the net-sweeping samples were used to examine pollen loads on their bodies or stomach contents. All collections for trees #229 and #1001, and seven collections among 11 for tree #225 were classified to order, and to family for Coleoptera. All insects collected by flower-collection were classified to order and to species for Thysanoptera. In addition to the above sampling in the crown, abscised corollas fallen on a terrace of the tower (25 m above the ground) were collected to examine insects in the corollas at 11:00 on 14 May.

Finally, 20-25 open-pollinated flowers were collected and fixed in FAA (formalin; acetic acid; alcohol) at 18:00 and 22:00 on 13 May, 03:00, 06:00, 10:00, and 15:00 on 14 May, and 12:00 on 16 May. Pollen grains on stigmas were counted under a microscope. Rank correlation between sampling time and the number of pollen grains on a stigma was examined by Spearman's rank correlation test, because intensity of pollinator activities might change in the course of the day. Flowers collected on 16 May were also examined for damage due to gnawing by beetles.

Pollination experiments

To examine the breeding system of *S. parvifolia* and the contributions of insect visitors to pollination, seven experiments were performed on tree #225:

(1) open: flowers on four inflorescences were left exposed permitting

unhindered insect visitation; **(2) untreated, bagged**: flowers on two inflorescences were bagged before the tree started blooming; **(3) open, flower-reduced**: flowers on three inflorescences were removed except for flowers which opened on 19-20 May as controls of experiments 4-7; **(4) self-pollinated (geitonogamous)**, **(5) cross-pollinated**: flowers on 11 inflorescences were hand-pollinated with geitonogamous pollen from different inflorescences on the same tree for experiment 4 (self-pollinated), or with cross pollen from trees #229 and #1001 for experiment 5 (cross-pollinated), sampled just before anthesis on 19-20 May: pollen was transferred using Chinese writing brushes, and all untreated flowers were removed; **(6) thrips-introduced**; and **(7) beetle-introduced**. Experiments 6 and 7 were made in the following manner twice, on 22 and 27 May: flower visitors were collected on tree #229 at 20:00 by sweeping four branches (about 200 open flowers on each) and separated thrips, beetles, and other insects. The thrips and beetles were each released separately into two tetron bags (TORAY, tetron®, number 9000) enclosing the inflorescences before anthesis on tree #225, and left for 2 days. All untreated flowers on the inflorescences were removed. This procedure resulted in introduction of 53-54 beetles or 18-37 thrips into each bag.

We monitored changes in the number of fruits on branches every 2 weeks until fruit dispersal in experiments 1 and 2, and until 32 days after flowering in experiments 3-7. In addition, I followed unbagged flowers and fruits on five inflorescences of tree #229 until seed dispersal.

To examine whether exclusion of flower visitors caused a decrease of fruit set, I compared fruit set in open and untreated, bagged flowers (experiments 1 and 2) on day 48 after flowering peak by Fisher's exact test. Then, fruit set in experiments 3-7 was compared with that in untreated, bagged flowers (experiment 2) on day 32 after flowering to investigate which treatments increased fruit set comparing with bagged, untreated flowers. At

that time, the fruits weighed 0.116 ± 0.039 g (dry mass, $N = 16$), 40% of the dry mass of mature fruits (0.271 ± 0.075 g, $N = 21$), and their sepals had turned from green to red.

Results

Flowering phenology and floral biology

Since monitoring of reproductive phenology began in June 1993, *Shorea parvifolia* flowered twice, 30 April–22 June 1996 and 19 September–7 November 1996. Flowering frequency was higher in larger trees: flowering occurred twice in the two emergent trees, once in the two canopy trees, and was lacking in the subcanopy trees (Table 4-1).

In the first flowering event in 1996, tree #225 flowered from 30 April to 10 June and reached a plateau from 14 to 28 May. The inflorescences are terminal or axially panicles with 150 ± 65 ($N = 8$) branchlets. A single branchlet of an inflorescence produces 4.6 ± 1.7 flowers ($N = 205$). Flowers are yellow, about 1.3 cm in diameter with a dry mass of 0.037 ± 0.0034 g ($N = 21$). The five revolute petals form a bowl-shaped structure at the center of the corolla, in which an ovoid ovary with a distinct stylopodium is located, surrounded by 15 stamens. The stamens are arranged in three verticils. Each stamen bears two-celled anthers, each with two thecae, and a terminal awn-like appendage, which becomes reflexed at anthesis. The pollen is smooth but slightly sticky, not dry, and not easily dislodged. The pendant flowers open around 18:00, releasing a strong, sweet scent. The anther thecae dehisce just before anthesis. The flowers do not secrete nectar. The corollas start to fall off in the following morning, while 68% of the expanded corollas remain in the crown until the next evening. They drop or are pushed off when new flowers open. By 23:00 on the next day, almost all the old flowers are shed.

Flower visitors and pollen on stigma

In net-sweeping, 66-85% of all insects identified were small beetles (< 5 mm) and 10-32% were thrips (Thysanoptera). The composition of the net-sweeping samples collected on different trees was almost the same at the level of orders, though the percentage of thrips was much higher in tree #229 (32%) than in the other trees (10-11%) (Table 4-2). Within Coleoptera, Chrysomelidae (42%) and Curculionidae (36%) were the most abundant (Table 4-3). Corylophidae was abundant (24%) on tree #1001, but were not recorded from the other two trees. In flower-collection samples, all of the collected insects were thrips (74%) or beetles (26%) (Table 4-4). The number of thrips in fallen corollas (0.014 thrips per corolla) was much lower than that in the flowers on the tree crown (0.30 thrips per corolla). Ten species from three families of thrips were found from the flower collection samples (Table 4-4). *Thrips hawaiiensis* accounted for 75% of all the thrips identified.

Table 4-2. Orders of the insects (%) collected by net-sweeping method on three trees of *Shorea parvifolia* (trees #225 and #229, 19 May; tree #1001, 16 and 20 May). The numbers of sampling times are shown in parentheses.

Insect order	Tree no.			Total
	#229 (1)	#225 (7)	#1001 (2)	
Orthoptera	0.7	0.0	0.0	0.2
Blattaria	0.0	0.3	0.9	0.3
Hemiptera	0.7	8.6	1.9	5.6
Thysanoptera	32.4	10.8	11.2	16.0
Coleoptera	66.2	74.7	85.0	74.4
Diptera	0.0	1.1	0.9	0.8
Hymenoptera	0.0	3.2	0.0	1.9
Lepidoptera	0.0	1.3	0.0	0.8
Total %	100.0	100.0	100.0	100.0
No. of insects	148	371	107	519

Chrysomelid beetles, especially several species of *Monolepta* (Galerucinae), were very frequently observed walking around and flying among inflorescences during the night. They were observed feeding on flower petals and pollen on the inner surface of the corolla. A considerable amount of pollen was found in their stomachs. Petals of *S. parvifolia* have a thin, frilled edge toward the apical half, and many beetles were found to feed on this part of the petal. Seventy-five percent of the 63 flowers collected at 12:00 had damaged apical petal fringes and 29% had damaged stigmas, but I observed no damage to the ovaries. Mating behavior of the beetles was not observed. Thrips were observed walking on the inflorescences and creeping into the corolla between the petals as soon as the petals unfurled at anthesis. However, after that time they rarely emerged from the corollas. Thirty percent ($N = 30$) of beetles and 12% ($N = 97$) of thrips carried pollen on their bodies.

Table 4-3. Families of flower-visiting beetles (%) collected by the net-sweeping method on three trees of *Shorea parvifolia* (tree #225 and #229, 19 May; tree #1001, 16 and 20 May). The numbers of sampling times are shown in parentheses.

Coleoptera Family	Tree no.			Total
	#229 (1)	#225 (7)	#1001 (2)	
Scarabaeidae	1.0	1.9	3.3	2.0
Nitidulidae	7.1	12.5	0.0	8.8
Cryptophagidae	4.1	0.4	0.0	1.1
Corylophidae	0.0	0.0	24.2	4.9
Coccinellidae	0.0	1.1	0.0	0.7
Chrysomelidae	57.1	31.4	60.4	42.8
Curculionidae	29.6	49.2	8.8	36.9
Other	1.0	3.4	3.3	2.9
Total	100.0	100.0	100.0	100.0
No. of insects	98	264	91	453

Table 4-4. Insects collected by flower-collection method on three trees of *S. parvifolia*. All the insects were thrips and beetles, and only the thrips were identified to species. In addition to the adult thrips, only one larva of *Phlaeothripidae* sp. was collected (four collections of 6-hour intervals, 16 May, tree #225).

Order		
	Suborder	
	Family	
	Species	N
Coleoptera		75
Thysanoptera		
	Terebrantia	
	Aeolothripidae	
	<i>Desmidothrips</i> sp. (<i>inanditus</i> ?)	3
	Thripidae	
	<i>Craspedothrips</i> <i>minor</i>	1
	<i>Ernothrips</i> sp. (<i>lobatus</i> ?)	1
	<i>Megalurothrips</i> <i>typicus</i>	5
	<i>Thrips</i> <i>coloratus</i>	25
	<i>Thrips</i> <i>hawaiiensis</i>	118
	<i>Thrips</i> sp. (<i>aleuritis</i> ?)	2
	<i>Thrips</i> sp. (<i>alius</i> ?)	1
	Tubulifera	
	Phlaeothripidae	
	<i>Hoplandrothrips</i> <i>flavipes</i>	1
	<i>Haplothrips</i> sp. (<i>tenuioennis</i> ?)	1
	Larva (species unknown)	1
	Not identified ^a	39
Total		273

^a Could not be identified because of bad specimen condition.

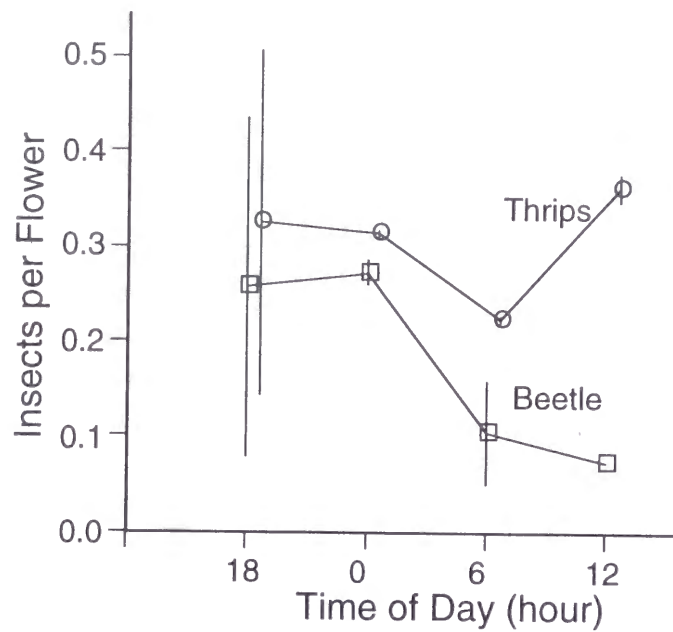


Fig. 4-1. Means and standard errors of the numbers of thrips (open circle) and beetles (open square) per flower in the crown estimated based on two sampling methods, net-sweeping and flower collection. The standard error for beetles at 1200 are not shown because only one net-sweeping sample is available.

The estimated number of thrips per flower (0.31) was 1.7 times larger than beetles (0.18). However, the beetles were three times more numerous at night than in the daytime, and their number was almost equal to the number of thrips at 00:00 (Fig. 4-1). Changes in the numbers of thrips samples were smaller than beetles. Higher density of beetles at night than in the daytime and smaller fluctuation in thrips density than that of beetles were showed by both sampling methods, net-sweeping and flower collection.

The number of pollen grains on the stigmas of open-pollinated flowers gradually increased following anthesis, particularly between 22:00 and 03:00, and rank correlation between sampling time and the number of pollen grains was significant (Spearman's coefficients of rank correlation: $r_s = 0.24$, $P = 0.003$, Fig. 4-2). The number of pollen grains per stigma showed great variation within

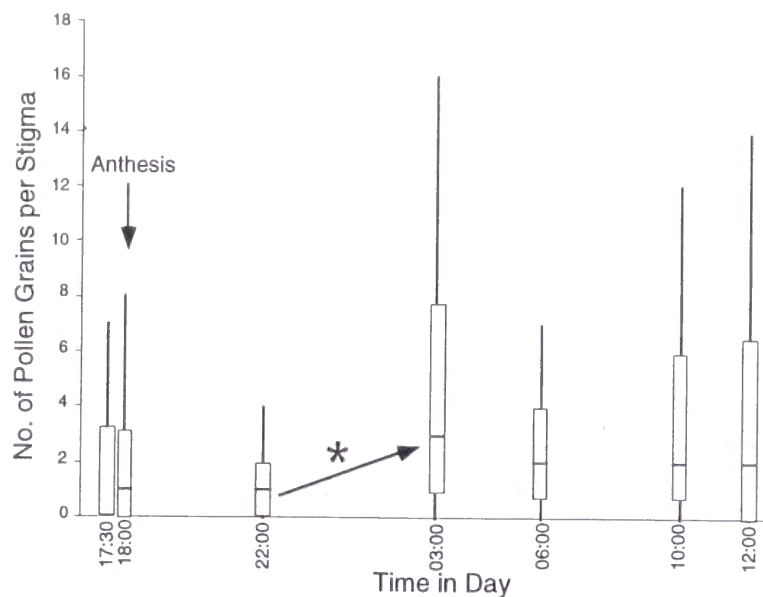


Fig. 4-2. Changes in the number of pollen grains on a stigma after flower opening. Maximum and minimum in each sample are shown by the upper and lower ends of vertical bar, 75 and 25% points are given by the upper and lower ends of box, and mode is shown by horizontal bar in the box. Considerable increase of pollen grains is indicated by an asterisk.

each sample, and 47% ($N = 17$) of the flowers collected at 17:30 just before anthesis, already had some self pollen on the stigma. The number slightly decreased between 03:00 and 06:00.

Changes in fruit numbers

Immature fruits on open inflorescences aborted continuously until day 48 after the flowering peak (Fig. 4-3). Only 0.7% of the original ovaries remained by that time. The first viable fruits were collected 93 day after flowering (23 August). If all fruits fallen before 23 August were immature, only 0.17% of the flowers gave rise to mature fruits. The number of fruits remaining on tree #229 decreased more quickly. However, mature fruits remained about 10 days longer on tree #229 than on tree #225 (Fig. 4-3).

Abortion in untreated, bagged inflorescences was much higher than in

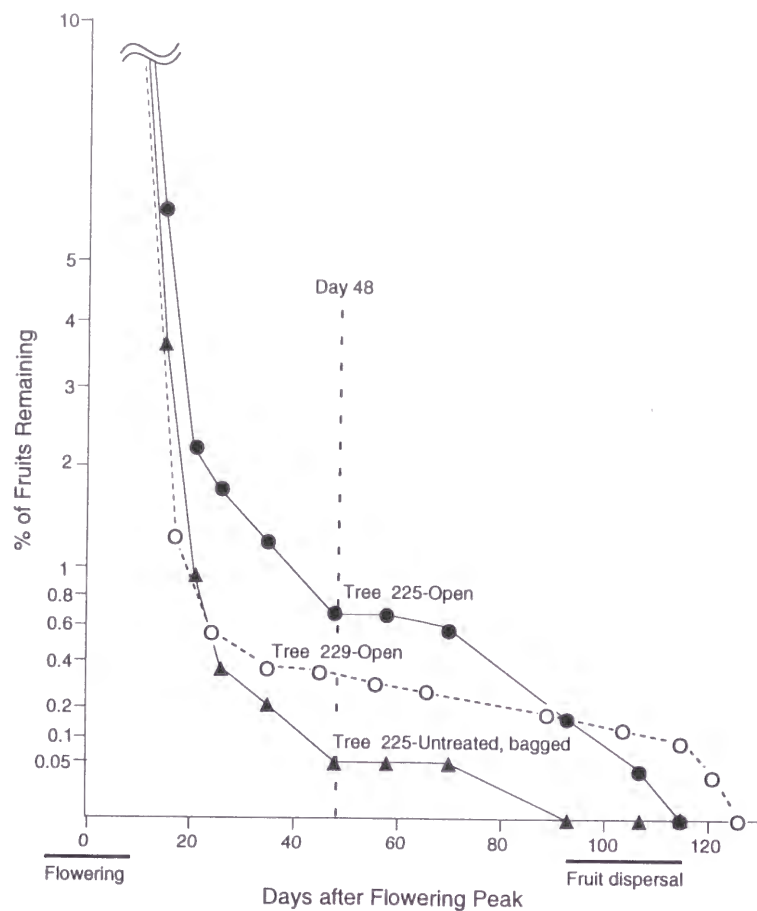


Fig. 4-3. Changes in percentage of the fruits remaining on untreated, bagged and open inflorescences. Arcsine transformation is used in the axis of percentage. Time point for comparison of fruit set is indicated by a dotted line.

open inflorescences (Fig. 4-3). The percentages of fruit set in bagged inflorescence at day 48 after flowering peak (0.05%) was significantly lower than that in open inflorescences (0.67%) (Fisher's exact test; $P < 0.001$). Only one fruit matured in bagged inflorescences.

Comparison of fruit set

The number of fruits decreased considerably up to day 21-24 after

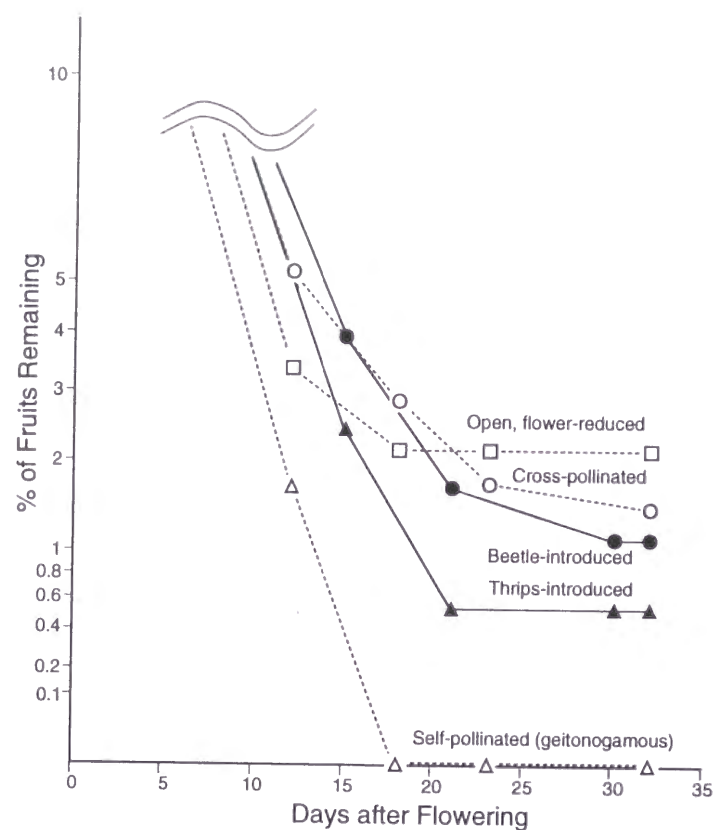


Fig. 4-4. Changes in percentage of the fruits remaining on open, flower-reduced, self- (geitonogamous) and cross-pollinated, and beetle- and thrips-introduced inflorescences resulting from pollination experiments 3-7. Arcsine transformation is used in the axis of percentage.

flowering in experiments 3-7, but the numbers more or less stabilized thereafter (Fig. 4-4). Observed fruit set was highest in open, flower-reduced inflorescences (2.17%, $N = 323$), followed by that in cross-pollinated ones (1.74%, $N = 345$), and fruit set in both the experiments was significantly higher than in untreated, bagged inflorescences (0.27%) ($P < 0.001$ for open, flower-reduced; $P = 0.003$ for cross-pollinated; Table 4-5). However, fruit set in self-pollinated (geitonogamous) inflorescences did not differ from that in bagged inflorescences.

Fruit set of both beetle-introduced (1.13%) and thrips-introduced

Table 4-5. Fruit set of the flowers in pollination experiments 3–7.

Percentages of the total flowers (N) remaining on the inflorescences 32 days after flowering are shown. Significance of difference from fruit set in untreated, bagged flowers (experiment 2) was examined by Fisher's exact test (one-sided).

Experiment	N	% fruit remaining on day 32	Significance of deviation (P)
3 Self-pollinated (geitonogamous)	176	0.00	0.636
4 Cross-pollinated	345	1.74	0.003
5 Open, flower reduced	323	2.17	0.000
6 Beetle-introduced	529	1.13	0.019
7 Thrips-introduced	368	0.54	0.327

flowers (0.54%) was between that of open flowers (1.44%) and untreated, bagged flowers (0.27%). Flowers in beetle-introduced bags had significantly higher fruit set than did untreated, bagged flowers ($P = 0.019$), but flowers in thrips-introduced bags did not (Table 4-5). Densities of introduced insects per flower per day were 0.81 for beetles and 0.60 for thrips. These are higher than the natural condition observed by net-sweeping and flower collection on the tree #225 (0.18 beetles and 0.31 thrips). The numbers of fruits fertilized per insect were 0.014 for beetles and 0.009 for thrips.

Discussion

Breeding system of S. parvifolia

The results of the pollination experiments show that the tree #255 received enough pollination service for outcrossing. Very low fruit set was characteristic of all treatments and has generally been observed by us and others (e.g., Chan 1981). Fruit set was significantly increased by application of

cross pollen but fruit set did not change by application of geitonogamous pollen. The results demonstrate that *S. parvifolia* is strongly self-incompatible, as are other species of *Shorea* (Chan 1981) and related genera (Momose *et al.* 1996). This is further supported by the fact that only a small proportion of fruits from untreated, bagged flowers remained until just before mature fruit dispersal, although nearly half of the flowers sampled just before anthesis had pollen grains on the stigma. In spite of the strong self-incompatibility, fruit set was not different between open and cross-pollinated flowers, probably because most functional pollination in open treatment was cross pollination.

The pollinators of S. parvifolia

Small beetles, particularly Chrysomelidae and Curculionidae, were the major flower visitors of *Shorea parvifolia* collected by the net-sweeping method on the three study trees, and the spectra of beetle families was not different among trees except for the occurrence of Corylophidae on one tree. On the other hand, thrips were the most abundant insects collected by flower collection. The density of thrips in the crown was greater than that of beetles if averaged throughout 24 hours, but beetles and thrips were equally abundant at night. Two other lines of evidence, higher mean pollen loads on beetles than on thrips and more frequent movements of beetles among flowers than thrips, suggest higher potential contribution of beetles to cross-pollination than thrips. However, the contribution of flower visitors to pollination cannot be measured only by their visitation frequency (Schemske & Horvitz 1984, and references therein), and the amount of body pollen is not always a good index of their ability to effect fruit set (Inouye *et al.* 1994). To evaluate this parameter, I performed introduction experiments of the two major flower visitors.

Bagged flowers onto which beetles had been introduced showed

significantly higher fruit set than untreated, bagged flowers, while bagged flowers onto which thrips had been introduced did not. Fruit set in beetle-introduced flowers showed higher fruit set than in thrips-introduced flowers. This demonstrates that the introduced beetles were more successful than thrips at depositing pollen on stigmas and fertilizing the flowers. The number of flowers fertilized per beetle was 1.5 times higher than that per thrips.

What was not incorporated into the experiments was proportions of self- and cross-pollen that insects carry under natural conditions, namely, the proportion of beetle or thrips individuals that move between conspecific trees each day because the beetles and thrips used in the experiments were artificially transferred between trees. Though movements of the beetles and thrips among trees were not observed, beetles seem more likely to move between conspecific trees than thrips. The number of beetles increased threefold at night compared to daytime, in spite of persistence of many corollas for > 24 hours in the crowns. Some thrips remained in fallen corollas.

The other problem is that net-sweeping, by which the flower visitors for the experiments were caught, may introduce pollen load artifacts for flower visitors. It may affect both the numbers of individuals with pollen load, and the result of experiment 7, in which flower visitors collected by net-sweeping were introduced into bagged inflorescences. However, even if the sampling caused pollen load artifacts, I believe that the difference between beetles and thrips in a pollen load is still meaningful because beetles and thrips were collected in the same method.

Nearly half of the flowers had pollen on their stigma before anthesis, and a significant increase of pollen grains was observed following anthesis. The slight decrease at 12:00 may be caused by earlier drops of fertilized flowers than unfertilized ones. The activity of thrips, which had a density of only 0.31 per

flower, could not be responsible for all the pollen on the stigmas. Dehiscence of the anthers before anthesis probably permits pollen to be shed on the stigma as well as inner surface of the corolla, though this is paradoxical in an obligate outcrosser. Scattered pollen on the inner surface of the corolla may be more easily attached to flower visitors than pollen remaining in the anthers. The increase of pollen grains on the stigma following anthesis may be brought about mainly by the beetles. Thrips was most active at the onset of anthesis, and between-flower movement of thrips was not observed thereafter, while the beetles were observed flying around the flowers throughout the night.

The contribution of beetles as pollinators at the study site, Lambir, Sarawak, was confirmed by the beetle-introduction experiment. The situation in Lambir seems to be different from that at Pasoh, Peninsular Malaysia, from where Appanah & Chan (1981) reported thrips pollination in six species of *Shorea* sect. *Mutica*. Beetles accounted for one-third of flower visitors at Lambir, and the density of thrips (0.31 thrips per flower) was much lower than that at Pasoh (2.4) where most flower visitors were thrips. However, I cannot eliminate the possibility that thrips contributed to pollination, because no statistical difference in fruit set was detected between thrips introduced flowers and open-pollinated ones.

Thrips often occur as general pollen feeders on various plant species (Kevan & Baker 1983; Kirk 1984). *Thrips hawaiiensis*, the most abundant thrips species on *S. parvifolia* at Lambir, has been collected on oil palm flowers (*Elaeis guineensis*, Palmae) in a plantation in Peninsular Malaysia (Syed 1979) and on *Lantana camara* (Verbenaceae) in India (Mathur & Mohan Ram 1978). They usually play a minor role as pollinators, although predominant thrips pollination has been reported for *Calluna* (Ericaceae) in the Faeroes, where weather condition and lack of larger insects prohibit pollination by other insects

(Hagerup 1950), and for Annonaceae (Webber & Gottsberger 1995; Momose *et al.* in press), Araceae (Rust 1980), Lauraceae (Norton 1984), and Winteraceae (Thien 1980; Pellmyr *et al.* 1990) in other regions with rich insect fauna. For a thrips-pollinated tree species in the understory of Lambir forest, *Popowia pisocarpa* (Annonaceae), Momose *et al.* (in press) suggested limited pollen dispersal by the thrips based on low fruit set of isolated trees. Thrips, with their oar-like wings, may be dispersed by local air drafts, including convectional movements: which are frequent in tropical forest canopies, especially during the day, but seldom penetrate the understory (Richards 1997).

S. parvifolia and beetle pollinators

Flowers of *S. parvifolia* have a character adapted to beetle pollination. The apical edge of their five petals is thin and soft, and damage by beetles is concentrated in that part of the petals. The apical region of the petals may be more attractive than stigmas or ovaries for the beetles. Moving from one petal to another of a flower or feeding on pollen on the inner surface of the corolla, beetles acquire pollen loads, and then deposited pollen on the stigma. These edible rewards for the beetles may promote pollination by both rewarding beetle visits and by reducing potential damage to stigmas and ovaries.

Beetles pollinate a wide range of plant species with various reproductive characters, and the specificity of the plant-pollinator interaction also varies (Endress 1994). Throughout the Lambir forest, many plant species are reported to be pollinated by beetles, especially in the Annonaceae (Momose *et al.* 1998b). These beetle-pollinated Annonaceae have more or less specialized relationships with their beetle pollinators and offer stigmatic secretions and/or mating sites to their pollinators (e.g., Gottsberger 1989a, 1990; Momose *et al.* 1998b). In contrast, many beetle species were collected on the flowers of *S.*

parvifolia, though a few species accounted for most visits. The flowers are exposed in the emergent layer and never act as a refuge for the beetles. Mating behavior of the beetles was not observed.

The life histories of *Monolepta* species, the beetle genus that was most abundant on the flowers of *S. parvifolia*, remain unknown. These beetles were collected outside the general flowering period by beating on *Shorea* leaves and are observed feeding on young leaves of *Shorea* and other dipterocarps, which are available all the year-round even in seasons out of general flowering periods (M. Yamauti, unpublished data).

Plant-pollinator interactions in *Shorea* at Lambir appear to be different from that observed in lowland dipterocarp forests in Peninsular Malaysia: there, *Shorea* species in the same section are pollinated by common pollinators, and the species in each section flower sequentially. In a case of *Shorea* sect. *Mutica*, sequential flowering brings about drastic increase of their pollinators, thrips with an extraordinary short generation time (about 8 days). Thrips populations large enough for their pollination are established in a few weeks (Ashton *et al.* 1988; Appanah 1990, 1993). At Lambir, in contrast, beetles were collected on the flowers of, and may pollinate nine *Shorea* species including species of sect. *Mutica* and other sections (Momose *et al.* 1998b). Thrips densities on their flowers were much lower than that observed in *Shorea* at Pasoh (Appanah & Chan 1981; Sakai, unpublished data).

How the beetles with longer generation time than thrips can offer enough pollination service to these *Shorea* species, which flower only in general flowering periods? *Monolepta* species collected on *S. parvifolia* flowers were found rather constantly in monthly light trap samples (T. Itioka, Nagoya University, unpublished data). Instead of such a drastic multiplication as thrips shows, the beetles probably respond to an abrupt increase of floral resource in a

general flowering by changing foods from dipterocarp leaves to flowers. For irregular, infrequent reproductions, *Shorea* species may rear the pollinators during non-general flowering periods by providing their leaves to the pollinators.

Chapter 5. General discussion

Comparison of plant phenology between Lambir and other study site

Intensity of plant reproductive activities in Lambir forest show 5-10-fold differences between general flowering period (GFP) and non-GFP in terms of the proportion of flowering plants, and the fluctuation has a cycle much longer than a year. Such supra-annual seasonality at the community level involving diverse plant species still has not been reported from forests other than dipterocarp forests in Southeast Asia. Comparative data are limited because this study is the first report to document plant reproductive phenology covering almost a complete cycle from one general flowering to another.

The percentage of plants in flower at any time was usually quite low in Lambir, compared with other tropical regions. In La Selva, Costa Rica, 8-28% of overstory trees in a wet forest and 9-30% of tree species in a dry forest may flower all year (Frankie *et al.* 1974). For shrubs and treelets in a tropical montane forest in Costa Rica, Koptur *et al.* (1988) reported larger figures (20-60%). In tropical montane and premontane forest in Rwanda, 10-50% of tree species were flowering all year round (Sun *et al.* 1996). Hilty (1980) reported that 25-40% of tree species always flowered in Pacific Colombia. In a forest with a severe dry season the number of flowering species often dropped to zero for a few dry months each year, but the number at other times was greater than 10% and sometimes exceeded 60% (Murali & Sukumar 1994). In contrast, Medway (1972) reported similar figures to those of Lambir from a lowland dipterocarp forest in peninsular Malaya. In most months 0-3% of species were flowering, while at most 35% of the species bloomed during GFP.

The low percentage of flowering individuals is mainly due to low flowering frequency (long flowering interval) and concentration of flowering events into GFP. General flowering type and temporal aggregation in

reproductive events were commonly found among species in various categories of taxonomic groups, life forms, pollination systems and fruit types. More than a half of the species under observation were supra-annual or general flowering species with a flowering interval longer than one year. A continuous flowering pattern (extended flowering with short interruptions) was rarely found. Only two species flowered continuously with shorter non-flowering periods. In contrast, a long-term survey (12 years) of flowering in lowland tropical rain forest from La Selva showed that more than half of the tree species observed have a sub-annual flowering cycle and 6% have extended flowering. Only 9% were categorized as supra-annual (Newstrom *et al.* 1994a, 1994b).

Dominance of species with longer flowering intervals in dipterocarp forests may be partly explained by absence of annual flowering cue. Although supra-annual seasonality at the community level is unique to lowland mixed dipterocarp forests, considerable variation in crop size among years is often reported from temperate and tropical forests (Kelly 1994; Wright 1998). Fluctuation in crop size may be related to fluctuation in environmental conditions, such as the amount of solar radiation (Wright 1998), or sometimes switching between mast and non-mast years, in which more than environmental variation involved, is observed (Kelly 1994). Occurrence of switching suggests that the plants adopt annual flowering cue, although one-year flowering cycle may be too short for those species. It may be because the annual cue is quite clear, reliable and regular. In contrast, in aseasonal climate as Lambir, there are no clear annual rhythm in climate, and plants may respond to flowering cue with longer but irregular intervals, because there are no other regular and reliable cues.

On the other hand, Janzen (1974) proposed poor soil condition in dipterocarp forests, comparing with African and neotropical forests, as one of

the factors for long flowering intervals. He also examined literature and indicated negative correlation between length of general-flowering intervals and soil richness. However, further quantitative data are needed to confirm relationship of flowering intervals and soil conditions. The other characteristics of general flowering, concentration of flowering events, i.e. inter-specific flowering synchronization, is discussed in detail in the last section of this chapter.

Plant reproductive phenology and pollination system

Observations have found three tactics of floral resource consumers to response to an abrupt increase of floral resource during GFP while maintaining their population during non-GFP: (1) immigration; (2) stabilization of fluctuating resource availability by storing excess resource; and (3) feeding niche shift.

Immigrating flower visitors are represented by giant honey bees (*Apis dorsata*). The seasonal migration of *A. dorsata* over 100 km between montane and lowland area reported from Sri Lanka (Koeniger & Koeniger 1980) demonstrates their ability to migrate a long distance. Around Canopy Biology Plot, several nests of *A. dorsata* were found only during or just after GFP (Nagamitsu 1998). Although *A. dorsata* store excess pollen and nectar in their nests, their nests usually do neither last more than a year nor support their population during non-GFP in the forest. The bees may adopted to general flowerings by immigration rather than by storing floral resource.

Stingless bees are resident bees in Lambir (Nagamitsu & Inoue 1997). Migration or absconding of stingless bees is rarely recorded (Michener 1974; but see Inoue *et al.* 1984a). General flowering may bring about a great increase of resources for stingless bees visiting a wide variety of flowers irrespective of the

principal pollinators, and an increase in their populations. Stingless bees store excess honey and pollen in their nests, stabilize the effects of temporal changes in floral resources at a colony level. A colony of stingless bees can survive for several years without resupply and maintain forager workers, which can quickly start foraging in response to an abrupt increase of ephemeral and massive floral resources in both GFP and non-GFP (Inoue *et al.* 1984b, 1990, 1993; Salamah *et al.* 1990). Dominance of highly socialized bees including the genus *Apis* in pollinators, comparing with Neotropical forest in Costa Rica, where medium to large anthophorid bees are dominant and *Apis* is absent, may be associated with unpredictable floral resource availability in the forests with general flowering phenomenon (Bawa *et al.* 1995; Kress and Beach 1994; Momose *et al.* 1998b).

Differences in flowering patterns between *Apis*-pollinated and small social bee-pollinated species can be explained by the migrating and resident habits of them. It is impossible for plants flowering during non-GFP to be pollinated by *Apis dorsata* because the population density of *A. dorsata* is extremely low during non-GFP. The tight relationships among general flowering, *Apis* bees and *Apis*-pollinated plants possibly have led to the large proportion of general flowering species and the drastic increase of flowering individuals during GFP in *Apis*-pollinated species. In contrast, increase of populations during GFP but persistence during non-GFP of stingless bees may be related to the flowering patterns in small social bee-pollinated species. The proportion of flowering individuals increased during GFP but did not drop to zero during non-GFP.

Feeding niche shift found in the beetle pollination in *Shorea* reported in Chapter 4 have never been known. Some beetles pollinating Dipterocarpaceae are herbivores, and feed on new leaves of dipterocarp trees during non-GFP

without dipterocarp flowers (Chapter 4; Sakai *et al.* 1999; M. Kato, M. Yamauti unpublished data), although life history of the beetles remains to be known. An increase of floral resources might cause their feeding niche shift. The pollination system may propose new adaptation of plants in aseasonal and unpredictable environment; for irregular, infrequent reproductions, *Shorea* species may rear the pollinators during non-GFP by providing their leaves to the pollinators.

Many other beetle pollinators are known to pollinate and to feed on floral resources of specific host plants (Gottsberger 1990). They hardly seem to respond to an increase of flowers other than those of their host plants, and their population is not maintained if flowering of their hosts occur at irregular and long intervals. The proportion of general flowering species in Annonaceae, in which most species have well-known specialized relationship with their beetle pollinators (Gottsberger 1989a, 1989b), was the smallest of all the taxonomic groups that I examined except *Ficus*. Non-dipterocarp beetle-pollinated plants did not show a sharp rise in the percentage of flowering individuals during GFP.

Of the plant groups that I examined, *Ficus* was unique since none of them belonged to the general flowering type, and the proportion of the individuals with syconia did not change significantly through the study period. The association between *Ficus* (Moraceae) and their pollinators, the fig-wasps (Agaonidae, Hymenoptera), involves a species-specific and unique pollination system (Galil & Eisikowitch 1968; Compton *et al.* 1996). Phenology of flower production at the population level must ensure survival of the pollinators if their obligate mutualistic relationship is to be maintained. This requirement may bring about the typical phenological pattern of *Ficus* found in tropical regions, which is annual or supra-annual flowering at the individual level integrated into a continual pattern at the population level (see citations in Table

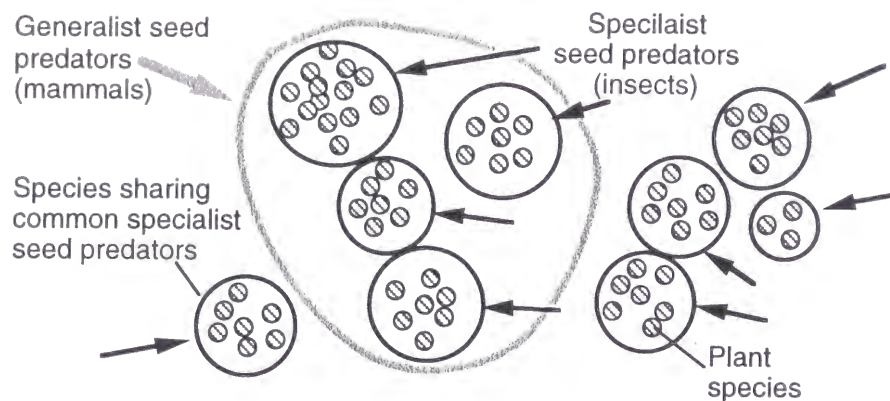
1 of Bronstein *et al.* 1990; Milton 1991).

Hypotheses for evolution of a general flowering

Janzen (1974) was apparently the first to evaluate ultimate causes of general flowering with synchronized flowering among many species. He suggested that seed predator or herbivore, especially mammals and birds who have general diet on fruits and seeds of a variety of species, could be the primary selective factor. Even if the predators disperse the seeds, large consumption of seeds by frugivores and granivores is detrimental. Losses to seed predators could be reduced by varying the seed crop size in space or time (Janzen 1971).

The observations reported in Chapter 3 indicated that satiation of generalist seed predators alone cannot explain general flowering at the community level. First, no large difference in flowering phenology was found among fruit types, although the animal-dispersed species had a slightly different flowering patterns from non-animal dispersal species. The predator satiation hypothesis assumes generalist fruit predators, mainly birds and mammals, as predators to be saturated. However, it is unreasonable to suppose that generalized vertebrate predators eat small seeds like those of orchids, or seeds in fruits offering special rewards for fruit dispersers, and yet these species also flowered heavier during GFP than during non-GFP. In addition, the second flowering peak was observed just after fruiting of the first flowering during GFP. Dayanandan *et al.* (1990) recorded a similar event among mast fruiting dipterocarps in Sri Lanka. In such a case vertebrate predator populations might become very high in several months after the first fruiting peak, so that predator satiation would not be effective in the second masting. Besides, the importance of general predators has not yet to be supported by field data.

A. Generalist and specialist predator satiation



B. Promotion of pollination

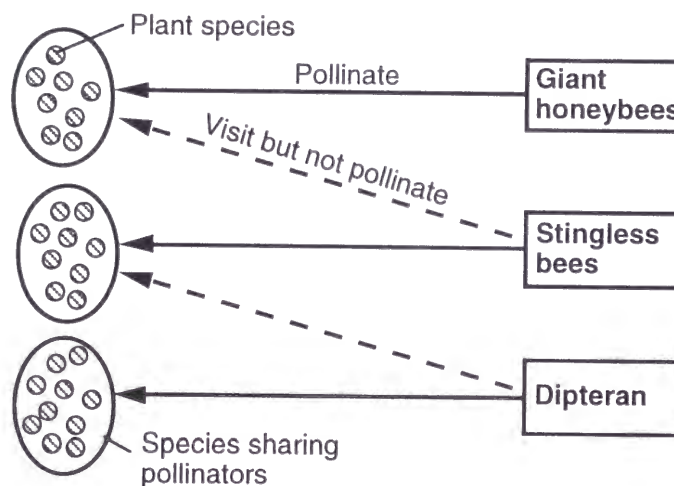


Fig. 5-1. Diagrams illustrating two possible factors for inter-specific synchronization in flowering and fruiting. **A.** Satiation of fruit predators increase survivorship of fruits and promote synchronization of fruiting among species sharing common seed predators. When the predator is generalist such as mammals (gray circle), synchronization occurs among wide range of species. In case the predators are specialist as insects, predator satiation promote flowering synchronization only among closely related plants attacked by the same specialist predators (black circle). **B.** Synchronized flowering among plants in the same pollination guild (a group of species which share common pollinators) can intensify pollinators' activities to bring about higher pollination success. Besides, flowering synchronization among species pollinated by (solid line) different pollinators may lead to higher pollination success due to interaction among plants, pollinators and flower visitors. Pollinators of some species may visit but rarely pollinate (dotted line) the other plants, but the plants would also contribute to population growth of the flower visitors. *Apis*-pollinated plants are exploited by stingless bees and thus contribute to the population growth of stingless bees. Thus, it is advantageous to stingless bee-pollinated species to flower together with *Apis* bee-pollinated plants. In turn, stingless-bee flowers may have an alternative effect on dipteran visitors.

However, predator satiation at the level of a species or a group of related species sharing common fruit predators can promote flowering synchronization among them. Fruit predators assumed in this case are specialists, mainly coleopteran and lepidopteran insects breeding in fruits or seeds. Some studies indicate that specialist predators of immature and mature fruits of dipterocarp trees caused considerable damage (Toy 1991; Momose *et al.* 1996). Toy (1991) showed that the sequential flowering of *Shorea* species during GFP resulted in sequential infection by a single weevil species, a specialist predator for immature fruits of *Shorea*. Nevertheless, specialist seed predator satiation alone does not explain synchronization among wide variety of species, because plants attacked by different fruit predators usually have little effects on each other while plants sharing common predators interact through the predators (Fig. 5-1A).

On the other hand, higher fruit sets in GFP than non-GFP found in general flowering and annual flowering species observed in Chapter 3 and found in *Shorea* by Yap & Chan (1990) indicate that other factors before fruit set cause higher reproductive success in GFP than non-GFP. Higher pollination success in GFP than non-GFP may arise to the difference. Only recently prevalence and importance of outcrossing even in tropical forests with high species richness and low population densities of most plant species have become recognized (Gan *et al.* 1977; Hamrick & Murawski 1994).

In most tropical plants, outcrossing is achieved by animal pollen vectors (Bawa *et al.* 1985; Kress *et al.* 1994; Momose *et al.* 1998b, Chapter 4 in this study). Aggregated flowering of various species sharing common pollinators may activate pollinators, and result in higher pollination success than isolated flowering. Although synchronized flowering of plants sharing common pollinators is often assumed to be disadvantageous because of competition for

pollinators, pollinator sharing sometimes works positive on the plants. Plants near the large resource patch of different plants sharing common pollinators may be visited by pollinators more often than isolated conspecifics (Thompson 1982). An increase of floral resources promote foraging activities of individual flower visitors, increases the density of flower visitors through immigration, population growth and feeding niche shifts. When competition for pollinators can be reduced through such mechanisms as fine temporal segregation in flowering time, synchronized flowering among species sharing the same pollinators will be advantageous for the plants.

Flowering synchronization among species with different pollination systems may also be promoted through interactions of plants and pollinators or flower visitors (Fig. 5-1B). Pollinators of some species may visit but rarely pollinate the other plants, but the plants would also contribute to population growth of the flower visitors. *Apis*-pollinated plants are often exploited by stingless bees once abandoned by *Apis* bees, which ignore small resource patch, and thus contribute to the population growth of stingless bees even they do neither contribute to nor interfere the pollination of the plant. Thus, it is advantageous to stingless bee-pollinated species to flower together with *Apis* bee-pollinated plants. In turn, stingless-bee flowers may have an alternative effect on other insect populations. In other words, even plants pollinated by different animals also interact each other through flower visitors and pollinators, while there may be little interactions through predators when the plants are attacked by different fruit predators.

It is unlikely that such flower visitor-mediated interactions between pollination guilds are symmetrical. *Apis dorsata* rarely visits small resource patches such as flowers pollinated by diverse insects. However, small diverse insects occasionally visit *Apis* bee-pollinated species. Some pollinators do not

have such interactions. In the case of a very specialized relationship such as figs and fig wasps, fig flowers are not visited by pollinators of other species and fig wasps do not visit other flowers at all. Flowers of Annonaceae and beetle pollinators also have a species-specific association. In such specific pollination systems, one plant species comprises one pollination guild, flowering should be fairly regular or continuous at the population level to maintain their pollinators. This may partly explain why figs and Annonaceae showed little or no increase in flowering intensity during GFP.

Paucity of possible flowering cues could be one of the driving forces for general flowering. Synchronization within a species is quite important, particularly for outcrossing species with low density, to assure cross-pollination. Besides, inter-specific synchronization in flowering and fruiting, which may bring about higher pollinator activities and less fruit predation, may be advantageous to plants. For intra-specific and/or inter-specific synchronization, the flowering trigger should be distinctive and reliable, to ensure that individuals in various microhabitat sense it equally and exactly at the same time. In addition, the switch is turned on at appropriate intervals, so that enough resource for flowering and fruiting is accumulated between reproductions. In the aseasonal tropical region of Lambir, possible climatic cues may be strictly limited. Correlations in temporal distributions of flowering events among general flowering, supra-annual and annual flowering types indicate a common flowering trigger. Existence of distinctive climatic cues with a one year cycle may explain dominance of the annual pattern in other tropical regions.

Then, what is the trigger for general flowering? Ashton *et al.* (1988) investigated the environmental cue for floral induction and general flowering using 11 years of meteorological data, and concluded that the most likely cue

was a drop in daily minimum temperature by roughly 2 °C. Our data monitoring climatic conditions in the crown of an emergent dipterocarp tree showed a drop in minimum temperature by up to 3°C 1–2 months before a general flowering began. To understand regularity and intervals of a drop of temperature, a possible cue for general flowering, climatological mechanisms for a drop of temperature should be further investigated.

Climate in Southeast Asia is strongly affected by El Niño Southern Oscillation phenomenon (Inoue *et al.* 1993). Ashton *et al.* (1988) showed that general flowering events in western peninsular Malaysia are significantly associated with El Niño. However, years of general flowering in peninsular Malaysia and Borneo differed site by site (Ashton *et al.* 1988). The drop of temperature just before general flowering in 1996 in Lambir and in Peninsular Malaysia (Pasoh and surrounded area, M. Yasuda, personal communication) occurred between El Niño events. Meteorological mechanism other than El Niño might cause the low temperature in the area (Yoshida 1998).

The three possible causes of general flowering, predator satiation, promotion of pollination, and a common trigger are not exclusive. Considering that pollinators and predators have also been adopted to general flowering phenomenon, it is not a simple problem which is the most important. Detailed observation of plant-pollinator interactions, response of flower visitors to general flowering, and examination of flowering triggers, as well as examination of relationship between plant characteristics and reproductive phenology as conducted in this study, and further accumulation of data on reproductive phenology may be needed to explore driving force and the scenario for the evolution of general flowering, and for conservation of lowland dipterocarp forests with extraordinary biodiversity.

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Appendix. A list of species with numbers of individual plants in the Canopy Biology Plot (CBP) observed from a canopy access system in the plot (TW) and observed from the forest floor (FF), and the plants observed from the Operation Raleigh Tower (ORT, TW) with life form types (LFM), species code, pollination system (PS) determined by (Det.) observations or collections of flower visitors or floral characters, fruit type (FR), and flowering type (FT).

Family	Species		Species code	LFM ^a	CBP		ORT	Total	Pollination		FR ^d	FT ^e
					TW	FF			PS ^b	Det ^c		
Anacardiaceae	<i>Bouea</i>	sp.	AC1	3			1	1	BT	e	a	G
	<i>Camptosperma</i>	<i>auriculatum</i>	AC2	G	4			4	BT	e	l	NF
	<i>Gluta</i>	<i>macrocarpa</i>	AC3	3	1			1	BT	e	l	NF
	<i>G.</i>	<i>wallichii</i>	AC4	4	1	1		2	BT	e	l	G
	<i>Mangifera</i>	<i>havilandii</i>	AC5	3			1	1	BT	e	a	NG
	<i>M.</i>	<i>magnifica</i>	AC6	4	2	2		2	BT	e	a	G
	<i>Melanochyla</i>	aff. <i>beccariana</i>	AC9	3	1			1	BT	e	l	NF
	<i>Parishia</i>	<i>sericea</i>	AC7	4	2			2	BT	e	l	NF
	<i>P.</i>	sp.	AC11	4	1			1	BT	e	l	NF
	<i>Swintonia</i>	<i>shwenenkii</i>	AC10	4			2	2	BT	e	l	NF
Annonaceae	Genus unknown	sp.	AC8	3			1	1	BT	e	l	NF
	<i>Artabotrys</i>	<i>venustus</i>	AN1	L	2			2	C	c	l	A
	<i>Cyathostemma</i>	sp.	AN2	L	1			1	C	c	l	NF
	<i>Desmos</i>	cf. <i>chinensis</i>	AN3	L	1			1	C	c	l	S
	<i>Enicosanthum</i>	<i>macranthum</i>	AN4	3		1		1	C	c	l	
	<i>Fissistigma</i>	<i>kingii</i>	AN5	L	1			1	C	e	l	
	<i>F.</i>	<i>latifolium</i>	AN7	L	2			2	C	c	l	NF
	<i>Mezzettia</i>	<i>havilandii</i>	AN8	4	1	1		2	C	e	a	
	<i>Monocarpia</i>	<i>euneura</i>	AN9	3	2			2	C	c	l	A
	<i>Polyalthia</i>	<i>hypoleuca</i>	AN11	3	1			1	C	e	a	
	<i>P.</i>	<i>rumphii</i>	AN13	2	1			1	C	c	a	NG
	<i>Pyramidanthe</i>	<i>prismatica</i>	AN10	L	4			4	C	c	l	G
	<i>Uvaria</i>	<i>desmoides</i>	AN6	L	1			1	C	c	l	A
Apocynaceae	<i>Anodendron</i>	<i>candolleianum</i>	AP1	L	1			1	BO	e	s	NG
	<i>Urceola</i>	sp.	AP3	L	1			1	BT	c	a	NF
	Genus unknown	sp.	AP2	L	1			1				
Aquifoliaceae	<i>Ilex</i>	sp.	AQ1	4	1	1		1	BT	e	a	NG
Araceae	<i>Potos</i>	sp.	AR1	E			1	1				NF
	<i>Scindapsus</i>	<i>coriaceus</i>	AR2	E	1			1				NF
Araliaceae	<i>Arthropphyllum</i>	<i>diversifolium</i>	AL2	4	1			1	BT	e	l	NF
	<i>Schefflera</i>	sp.	AL1	E	1			1	BT	e	a	
Ascrepiadaceae	<i>Gongronema</i>	sp.	AS1	L	2			2	BT	c	s	A
	<i>Hoya</i>	sp.	AS2	E	1			1	BT	e	s	G
Bombacaceae	<i>Coelostegia</i>	<i>griffithii</i>	BO1	4	1	2		2	C	c	l	NG
	<i>Durio</i>	sp.1	BO2	2	1			1			a	NF
	<i>D.</i>	sp.2	BO4	3		1		1			a	
	<i>D.</i>	sp.3	BO3	3		1		1			a	
Burseraceae	<i>Canarium</i>	<i>caudatum</i>	BU1	4	2	1		2	BT	c	a	NG
	<i>C.</i>	<i>denticulatum</i>	BU2	3	1			1	DI	c	a	G
	<i>C.</i>	<i>pilosum</i>	BU3	3	1			1	BT	e	a	NF
	<i>C.</i>	sp. C by Kochuman	BU6	3	2			2	BT	e	a	NF
	<i>C.</i>	sp.	BU18	4			1	1			a	NF
	<i>Dacryodes</i>	<i>incurvata</i>	BU9	4		1	1	2	BT	c	a	G
	<i>D.</i>	sp.	BU8	3	1			1	BT	e	a	NF
	<i>Santiria</i>	<i>griffithii</i>	BU10	4	1			1	BT	c	l	G

^a 2, understory (2.5–12.5 m); 3, subcanopy (12.5–27.5 m); 4, canopy (27.5–42.5 m); 5, Emergent (> 42.5 m);

G, gap tree; L, liana; E, epiphyte.

^b See Table 3-3.

^c e, estimated by floral characters; c, determined by collection of flower visitors; o, determined by observation of flower visitors.

^d a, animal dispersed; l, large fruit; s, small fruit.

^e S, subannual; A, annual; G, general flowering; NG, supra-annual flowering; NF, no flowering.

Appendix. (Continued, 1)

Family	Species		Species code	LFM ^a	CBP		ORT	Total	Pollination		FR ^d	FT ^e
					TW	FF			PS ^b	Det ^c		
Burseraceae	<i>Santiria</i>	<i>laevigata</i>	BU11	4	1	1		1	BT	c	1	NG
	<i>S.</i>	<i>mollis</i>	BU12	3	4	1		4	BT	e	1	A
	<i>S.</i>	sp. G by Kochuman	BU14	3			1	1	BT	e	1	G
	<i>S.</i>	<i>tomentosa</i>	BU5	4		1		1	BT	e	1	
	<i>Scutinanthe</i>	<i>brunnea</i>	BU15	5		2		2	BT	e	a	
	Genus unknown	sp.1	BU7	3			1	1	BT	e		NF
		sp.2	BU17	4	2	1		3	BT	e		G
	<i>Triomma</i>	<i>malaccensis</i>	BU22	5	1	1		1	DI	c	s	G
	Celastraceae	<i>Lophopetalum</i>	<i>glabrum</i>	CE1	3	3			3	BT	c	s
<i>L.</i>		<i>multinervium</i>	CE2	4	1						s	G
Chrysobalanaceae	<i>Atuna</i>	<i>excelsa</i>	CH1	3	1			1	BA	e	1	NF
	<i>Parastemon</i>	<i>urophyllum</i>	CH2	4	2	1		2	BA	o	1	G
Compositae	<i>Vernonia</i>	<i>arborea</i>	CM1	3	1			1	BA	e	s	G
Connaraceae	<i>Agelaea</i>	<i>borneensis</i>	CN2	L	1			1	BT	e	a	G
	<i>A.</i>	<i>macrophylla</i>	CN1	L	1			1	BT	e	a	NF
	<i>Connarus</i>	<i>euphlebius</i>	CN3	2	1			1	BT	e	a	G
Convolvulaceae	<i>Erycibe</i>	sp.	CV1	L	1			1	BT	c	a	NG
Crypteroniaceae	<i>Crypteronia</i>	<i>griffithii</i>	CR1	3	2			2	BT	c	s	NG
Dilleniaceae	<i>Tetracera</i>	<i>macrophylla</i>	DL1	L	1			1	BA	e	a	NF
Dipterocarpaceae	<i>Cotylelobium</i>	<i>melanoxyton</i>	DP1	5	1	1		1			1	NG
	<i>Dipterocarpus</i>	<i>acutangulus</i>	DP7	5	2	1	1	3	C	e	1	G
	<i>D.</i>	<i>geniculatus</i>	DP5	5	5	3	1	7	C	c	1	G
	<i>D.</i>	<i>globosus</i>	DP6	5			4	4	BA	c	1	G
	<i>D.</i>	<i>pachyphyllus</i>	DP8	5	13	10		15	L	c	1	G
	<i>D.</i>	<i>palembanicus</i>	DP4	4	6	1		6	C	c	1	G
	<i>D.</i>	<i>tempehes</i>	DP9	5	1	1		1	BA	c	1	G
	<i>Dryobalanops</i>	<i>aromatica</i>	DP10	5	9	9	2	14	BA	c	1	G
	<i>D.</i>	<i>lanceolata</i>	DP11	5	5	10		13	BA	c	1	G
	<i>Hopea</i>	<i>griffithii</i>	DP12	3	3			3	C	e	1	NG
	<i>Parashorea</i>	<i>lucida</i>	DP13	5			1	1	BA	o	1	NG
	<i>Shorea</i> sect.	<i>confusa</i>	DP26	5	1	1		1	C	c	1	G
	<i>Anthoshorea</i>											
	<i>S.</i>	<i>ochracea</i>	DP43	5	1	1		1	C	c	1	G
	<i>S.</i> sect.	<i>bullata</i>	DP27	5	6	4		6	C	c	1	G
	<i>Brachypterae</i>											
	<i>S.</i>	<i>fallax</i>	DP33	5	2	1		2	C	e	1	G
	<i>S.</i>	<i>kunstleri</i>	DP37	5		4		4	C	c	1	
	<i>S.</i>	<i>scaberrima</i>	DP49	5	1			1	C	e	1	NF
	<i>S.</i>	<i>smithiana</i>	DP51	5	11	9		13	C	c	1	G
	<i>S.</i> sect. <i>Mutica</i>	<i>acuta</i>	DP23	5			1	1	C	e	1	NF
	<i>S.</i>	<i>curtisii</i>	DP29	5	1	2	2	5	C	e	1	G
	<i>S.</i>	<i>ferruginea</i>	DP34	5	5	4		6	C	c	1	G
	<i>S.</i>	<i>leprosula</i>	DP38	5	2	1		2	C	e	1	G
	<i>S.</i>	<i>macroptera</i> var. <i>baillonii</i>	DP40	5	3	1		3	C	e	1	NF
	<i>S.</i>	<i>macroptera</i> var. <i>macropterifolia</i>	DP41	5	3	1		3	C	c	1	G
	<i>S.</i>	<i>parvifolia</i>	DP44	5	9	8		11	C	c	1	G
	<i>S.</i>	<i>quadrinervis</i>	DP46	5	1	1	1	2	C	e	1	NF
	<i>S.</i>	<i>slootenii</i>	DP50	5	1	1		1	C	e	1	NF
	<i>S.</i> sect.	<i>macrophylla</i>	DP39	5	2	1		3	C	c	1	NF
	<i>Pachycarpae</i>											
	<i>S.</i>	<i>pilosa</i>	DP45	5	6	6		6	C	c	1	G
	<i>S.</i>	<i>beccariana</i>	DP24	5	5	7		9	C	c	1	A
	<i>S.</i> sect.	<i>faguetiana</i>	DP14	4	2	2		3	C	e	1	G
		<i>Richetioides</i>										

Appendix. (Continued, 2)

Family	Species	Species code	LFM*	CBP		ORT	Total	Pollination		FR ^d	FT ^e
				TW	FF	TW		PS ^b	Det ^c		
Dipterocarpaceae	S. sect. <i>xanthophylla</i>	DP53	5	1	1		1	C	c	l	G
	<i>Richetioides</i>										
	S. sect. <i>Rubella</i>	DP47	5			2	2	C	e	l	NG
	S. sect. <i>Shorea</i>	DP25	4	4			4	C	e	l	NF
	S.	DP30	5	3	3		4	C	e	l	G
	S.	DP32	5	3	1		3	C	c	l	G
	S.	DP35	5	2	1		2	C	c	l	G
	S.	DP42	5			1	1	C	e	l	G
	S.	DP52	5	4	3		5	C	c	l	G
	<i>Vatica</i>	DP56	4	1			1	C	e	l	G
	V.	DP54	4	2			2	C	c	l	NG
	V.	DP55	4			3	3	C	e	l	NG
Ebenaceae	<i>Diospyros</i>	EB1	3	1			1	C	e	l	NG
	D.	EB2	2	1			1	C	e	l	NF
Elaeocarpaceae	<i>Elaeocarpus</i>	EL1	3	1			1	BT	c	a	A
	<i>Sloanea</i>	EL2	3	1			1	BT	e	s	NF
Euphorbiaceae	<i>Blumeodendron</i>	EU1	4	2			2	BT	e	l	NG
	<i>Cephalomappa</i>	EU3	4	1			1	DI	c	l	G
	<i>Cleistanthus</i>	EU5	3	1			1	BT	e	l	NF
	C.	EU7	3	1			1	BA	c	l	G
	C.	EU8	3	1			1	BT	c	l	G
	C.	EU6	3	3			3	BA	e	l	G
	<i>Drypetes</i>	EU11	4	1			1	DI	e	l	G
	D.	EU12	2		5		5	DI	c	a	
	D.	EU10	3	1			1	DI	e	l	S
	D.	EU4	2	1			1	DI	e	l	NF
	<i>Endospermum</i>	EU13	G	1			1	BT	e	l	S
	<i>Glochidion</i>	EU14	2	1			1	BT	e	a	NF
	<i>Koiloclepa</i>	EU15	3	5			5	BT	c	l	G
	<i>Macaranga</i>	EU19	G	1			1	BT	e	a	NF
	M.	EU16	G	1			1	BT	e	a	NF
	M.	EU17	G	13			13	BT	e	a	A
	M.	EU20	G	3			3	BT	e	a	G
	M.	EU23	2	1			1	BT	e	a	G
	<i>Mallotus</i>	EU25	4	5	2		6	BT	e	l	G
	M.	EU24	3	2			2	BT	c	l	G
	<i>Omphalea</i>	EU26	L	2			2	BT	e	l	S
	<i>Pimelodendron</i>	EU27	3			1	1	BT	e	a	G
	<i>Tapoides</i>	EU9	3	3			3	DI	c	l	G
	<i>Trigonoppleura</i>	EU22	3	1			1	BA	c	a	G
Fagaceae	<i>Lithocarpus</i>	FA2	4	1			1	DI	c	l	A
	L.	FA1	3	1			1	DI	e	l	
	L.	FA3	4		1		1	DI	e	l	
	<i>Quercus</i>	FA4	3	1			1	DI	e	l	
Flacourtiaceae	<i>Hydnocarpus</i>	FL1	4		1		1	DI	e	l	
Guttiferae	<i>Calophyllum</i>	GU1	4			1	1	BA	e	l	G
	C.	GU4	4		1		1	BA	e	l	
	C.	GU2	4	1		1	2	BA	e	l	NG
	C.	GU3	2	1			1	BA	e	l	NF
Guttiferae	<i>Garcinia</i>	GU5	3			1	1	BT	e	a	
	G.	GU6	4	1	1		1	BT	e	a	NG
	<i>Mesua</i>	GU8	4	1			1	BA	e	l	NG
Icacinaceae	Genus unknown	IC1	L	4			4	C	c	a	G
Ixonanthaceae	<i>Allantospermum</i>	IX1	4	7		2	9	BA	c	l	G

Appendix. (Continued, 3)

Family	Species		Species code	LFM*	CBP		ORT	Total	Pollination		FR ^d	FT*
					TW	FF			PS ^b	Det ^c		
Lauraceae	<i>Alseodaphne</i>	<i>insignis</i>	LA5	4	2	1		2	BT	e	a	NG
	<i>Beilschmiedia</i>	<i>phoebeopsis</i>	LA7	4	1			1	BT	e	a	NG
	<i>B.</i>	<i>turfosa</i>	LA8	4		1		1	BT	e	a	
	<i>Cinnamomum</i>	<i>javanicum</i>	LA1	3	1			1	BT	e	a	NG
	<i>Endiandra</i>	<i>clavigera</i>	LA2	3	1			1	DI	c	a	S
	<i>Eusideroxylon</i>	<i>zwageri</i>	LA3	4		4		4			a	
	<i>Litsea</i>	<i>petiolata</i>	LA4	4	1	1		1	BT	e	a	A
	<i>Phoebe</i>	<i>sterculioides</i>	LA9	4		1		1	BT	e	a	
	Genus unknown	sp.	LA6	4	1			1			a	NG
Lecythidaceae	<i>Barringtonia</i>	<i>curranii</i>	LC1	3	1	1		1	L	e	l	G
Leguminosae	<i>Archidendron</i>	<i>microcarpum</i>	LG11	3	1			1	BA	c	a	NG
	<i>Callerya</i>	<i>niewenhuissii</i>	LG28	L	2			2	BO	c	l	NG
	<i>C.</i>	<i>vasta</i>	LG9	4	3	4		6	BO	c	l	G
	<i>Crudia</i>	sp.	LG3	4	1			1	BA	e	l	NF
	<i>Dialium</i>	<i>indicum</i>	LG2	4	1	1		1	BA	e	a	
	<i>D.</i>	<i>kustleri</i>	LG4	4	1			1	BA	e	a	NF
	<i>D.</i>	<i>platysepalum</i>	LG1	4	1	1		1	BA	e	a	NG
	<i>D.</i>	<i>turbinatum</i>	LG5	4	1			1	BA	e	a	NF
	<i>Koompassia</i>	<i>excelsa</i>	LG7	5	3	1		3	BA	e	s	G
	<i>K.</i>	<i>malaccensis</i>	LG8	5	3	3		3	BA	e	s	G
	<i>Parkia</i>	<i>singularis</i>	LG12	3	1			1	M	o	l	NG
	<i>P.</i>	<i>speciosa</i>	LG10	3	1			1	M	o	l	G
	<i>Sindora</i>	<i>beccariana</i>	LG13	5	1	1		1	BT	c	l	NG
	<i>S.</i>	<i>irpicina</i>	LG14	5		1		1	BT	c	l	
	<i>S.</i>	<i>vertina</i>	LG15	5	1	1		1	BT	c	l	NF
	<i>Spatholobus</i>	<i>ferrugineus</i>	LG25	L	1		1	2	BA	c	s	NG
	<i>S.</i>	<i>macropterus</i>	LG24	L	1			1	BA	c	s	NF
	<i>S.</i>	<i>multifolius</i>	LG26	L	1			1	DI	c	s	G
	<i>S.</i>	<i>auricomus</i>	LG20	L	1			1				NF
	<i>S.</i>	sp.1	LG17	L	1			1	BA	e	s	G
	<i>S.</i>	sp.2	LG18	L	1			1	BA	e	s	NG
	Genus unknown	sp.1	LG19	L	1			1				NF
		sp.2	LG22	L	1			1				NF
		sp.3	LG21	L	1			1				NF
		sp.4	LG23	L	1			1				NF
Linaceae	<i>Indorouchea</i>	<i>griffithiana</i>	LI1	L	1			1				NF
Loganiaceae	<i>Strychnos</i>	<i>polytrichantha</i>	LO1	L	1			1			l	NF
Loranthaceae	<i>Amylothea</i>	<i>duthieana</i>	LR2	E			3	3	A	c	a	A
	<i>Trithecanthera</i>	<i>xiphostachys</i>	LR1	E	1			1	A	c	a	A
	Genus unknown	sp.	LR5	E	1			1	A	e	a	S
Magnoliaceae	<i>Talauma</i>	<i>gigantifolia</i>	MG1	2	1			1	C	e	a	NF
Melastomataceae	<i>Diplectria</i>	<i>stipularis</i>	MS2	L	1			1	BT	e		
	<i>Memecylon</i>	sp.	MS1	3	1			1	BT	e	a	NF
	Genus unknown	sp.	MS3	L	1			1				A
Meliaceae	<i>Aglaia</i>	<i>korthalsii</i>	ML4	4		1		1	BT	e	a	
	<i>Chisocheton</i>	<i>sarawakensis</i>	ML1	3	1			1	BO	e	a	G
Menispermaceae	<i>Coscinium</i>	<i>wallichianum</i>	MN1	L	1			1				
Moraceae	<i>Artocarpus</i>	<i>anisophyllus</i>	MO1	4		2	2	4	DI	e	a	NF
	<i>A.</i>	<i>dadah</i>	MO2	4	1			1	DI	e	a	NF
	<i>A.</i>	<i>elasticus</i>	MO3	4	1	2		3	DI	c	a	G
	<i>A.</i>	<i>integer</i>	MO4	4	1	3		3	DI	c	a	NF
	<i>A.</i>	<i>melinoxylus</i>	MO7	4		1		1	DI	e	a	
	<i>A.</i>	<i>nitidus</i>	MO5	4	1			1	DI	e	a	A
	<i>A.</i>	<i>odoratissimus</i>	MO6	4	1	1	1	2	DI	c	a	G

Appendix. (Continued, 4)

Family	Species		Species code	LFM ^a	CBP		ORT	Total	Pollination		FR ^d	FT ^e
					TW	FF			PS ^b	Det ^c		
Moraceae	<i>Artocarpus</i>	<i>tamaran</i>	MO8	4		1		1	DI	e	a	
	<i>Ficus</i>	<i>benjamina</i>	MO13	L		1		1	F	e	a	
	<i>F.</i>	<i>binnendykii</i>	MO19	L	1			1	F	e	a	A
	<i>F.</i>	<i>consociata</i>	MO15	L	1			1	F	e	a	S
	<i>F.</i>	<i>deltoidea</i>	MO9	E			1	1	F	e	a	S
	<i>F.</i>	<i>kerkhovenii</i>	MO14	L	3	2		4	F	e	a	S
	<i>F.</i>	<i>microcarpa</i>	MO20	L	1			1	F	e	a	
	<i>F.</i>	<i>pellucidopunctata</i>	MO18	L	1			1	F	e	a	A
	<i>F.</i>	<i>subcordata</i>	MO10	L	1			1	F	e	a	A
	<i>F.</i>	<i>sumatrana</i>	MO11	L	1			1	F	e	a	A
	<i>F.</i>	<i>xylophylla</i>	MO16	L	2			2	F	e	a	NG
Myristicaceae	<i>Prainea</i>	<i>frutescens</i>	MO22	3	1			1	DI	e	l	NF
	<i>Gymnacranthera</i>	<i>contracta</i>	MY1	4	2			2	C	c	a	A
	<i>Horsfieldia</i>	<i>grandis</i>	MY3	3	1			1	O	c	a	G
	<i>H.</i>	<i>pallidicaula</i>	MY5	3	1			1	O	e	a	
	<i>H.</i>	<i>polyspherula</i>	MY4	3	1			1	O	e	a	
	<i>Knema</i>	<i>cinerea</i>	MY17	4		1		1	C	c	a	
	<i>K.</i>	<i>furfuracea</i>	MY6	3	1			1	C	e	a	NF
	<i>K.</i>	<i>laterica</i>	MY7	3	2			2	C	e	a	G
	<i>K.</i>	<i>latifolia</i>	MY8	3	3			3	C	c	a	A
	<i>K.</i>	<i>pedicellata</i>	MY10	3	1			1	C	e	a	G
	<i>K.</i>	<i>sp.1</i>	MY12	3	1			1	C	e	a	A
	<i>K.</i>	<i>sp.2</i>	MY9	3	1			1	C	e	a	NG
	<i>K.</i>	<i>sp.3</i>	MY11	2	1			1	C	e	a	NF
	<i>Myristica</i>	<i>malaccensis</i>	MY13	3	1			1	C	e	a	NF
	<i>M.</i>	<i>villosa</i>	MY15	4	2			2	C	e	a	A
	<i>M.</i>	<i>sp.</i>	MY14	4	1	1		1	C	e	a	A
Myrsinaceae	<i>Ardisia</i>	<i>macrophylla</i>	MR1	3	1			1	A	o	a	G
Myrtaceae	<i>Eugenia</i>	<i>ochneocarpa</i>	MT4	3			1	1	DI	e		A
	<i>E.</i>	<i>ros lenta</i>	MT9	4	1			1	DI	e		NF
	<i>E.</i>	<i>subrufa</i>	MT5	4	2	2		2	DI	c		G
	<i>E.</i>	<i>sp.1</i>	MT6	4	1			1	DI	e		NF
	<i>E.</i>	<i>sp.2</i>	MT1	3			1	1	DI	e		G
	<i>E.</i>	<i>sp.3</i>	MT2	4		1		1	DI	e		
	<i>E.</i>	<i>sp.4</i>	MT3	4	2	1		3	DI	c	l	NG
	<i>E.</i>	<i>sp.5</i>	MT7	3	1			1	DI	e		NF
	Genus unknown	<i>sp.</i>	MT8	4	1			1	DI	e		G
Olacaceae	<i>Ochanostachys</i>	<i>amentacea</i>	OL1	3	1			1	BT	e	a	G
	<i>Scorodocarpus</i>	<i>borneensis</i>	OL2	4	1			1	BT	c	l	NG
Orchidaceae	<i>Trias</i>	<i>sp.</i>	OR1	E			1	1	BA	c	s	G
	Genus unknown	<i>sp.1</i>	OR5	E			1	1			s	NF
		<i>sp.2</i>	OR6	E	1			1			s	
		<i>sp.3</i>	OR7	E	1			1			s	NF
		<i>sp.4</i>	OR8	E	1			1			s	NF
		<i>sp.5</i>	OR9	E	1			1			s	NF
		<i>sp.6</i>	OR10	E	1			1			s	A
		<i>sp.7</i>	OR11	E	1			1			s	G
		<i>sp.8</i>	OR12	E	1			1			s	G
		<i>sp.9</i>	OR2	E	1			1			s	G
		<i>sp.10</i>	OR3	E	1			1			s	NG
		<i>sp.11</i>	OR4	E	1			1			s	
Pandanaceae	<i>Freyeinetia</i>	<i>winkleri</i>	PA1	E	2			2			a	NG
Piperaceae	<i>Piper</i>	<i>sp.</i>	PI1	L	1			1	DI	e	l	A
Rhizophoraceae	<i>Carallia</i>	<i>brachiata</i>	RH1	3	1			1	DI	c	a	S

Appendix. (Continued, 5)

Family	Species		Species code	LFM*	CBP		ORT	Total	Pollination		FR ^d	FT ^e
					TW	FF	TW		PS ^b	Det ^c		
Rubiaceae	<i>Pouterandia</i>	<i>anisophylla</i>	RU1	2	1			1	BO	e	l	NG
	<i>Randia</i>	sp.	RU2	L	1			1			l	A
	<i>Uncaria</i>	<i>longifolia</i>	RU3	L	2			2	DI	c	s	A
	U.	sp.1	RU7	L			1	1			s	A
	U.	sp.2	RU5	3	1			1			s	A
Sapindaceae	<i>Nephelium</i>	<i>cuspidatum</i>	SD1	4		1		1	BT	c	a	
	<i>Pometia</i>	<i>pinnata</i>	SD2	3	3	2		4	BT	c	a	G
	<i>Xerospermum</i>	<i>laevigatum</i>	SD3	3	1			1	BT	e	a	G
Sapotaceae	<i>Ganua</i>	<i>beccariana</i>	SP5	4	3			3	M	o	a	NF
	G.	<i>hirtiflora</i>	SP2	4		1		1			a	
	G.	sp.	SP1	4		1		1	M	e	a	
	<i>Palaquium</i>	<i>calophyllum</i>	SP6	4		1		1	BT	e	a	
	P.	sp.	SP3	5	1	1		1			a	G
	Genus unknown	sp.	SP4	4		1		1			a	
	<i>Simarouba</i>	<i>malayana</i>	SM2	4		1		1			l	
Sterculiaceae	<i>Quassia</i>	<i>borneensis</i>	SM1	5	2	2		2	DI	c	l	A
	<i>Heritiera</i>	<i>borneensis</i>	ST2	4	2	1		2	C	c	l	NG
	H.	<i>impressinervia</i>	ST9	5		1		1	C	e	l	
	H.	<i>sumatrana</i>	ST1	5	4	3		5	C	c	l	G
	H.	sp.	ST4	5	1			1	C	e	l	
	<i>Pterocymbium</i>	<i>tubulatum</i>	ST7	G		1		1	BA	c	l	
	<i>Pterospermum</i>	<i>fuscum</i>	ST5	4		1		1	M	e	s	
	<i>Scaphium</i>	<i>borneensis</i>	ST6	5			3	3	BA	c	l	G
	S.	<i>longipetiolatum</i>	ST8	4	2	2		3	BT	c	l	G
	<i>Sterculia</i>	sp.	ST10	2		1		1	C	e	l	
Theaceae	<i>Eurya</i>	<i>acuminata</i>	TH1	3	1			1	BT	c	a	A
Thymelaeaceae	<i>Amyxa</i>	<i>pluricornis</i>	TY3	3	1			1	DI	e	a	G
	<i>Gonystylus</i>	<i>forbesii</i>	TY1	3			1	1	DI	e	a	G
	G.	<i>micranthus</i>	TY2	L	1			1	DI	e	a	
Tiliaceae	<i>Linostoma</i>	<i>pauciflorum</i>	TY4	3	1			1	DI	e	a	NG
	<i>Pentace</i>	<i>adenophora</i>	TL1	3			1	1	BT	e	s	NF
	<i>Schoutenia</i>	<i>glomerata</i>	TL2	4	2			2	DI	c	s	NF
Ulmaceae	<i>Giloniera</i>	<i>nervosa</i>	UL1	G	1			1				NG
Verbenaceae	<i>Callicarpa</i>	<i>pentandra</i>	VR1	L	1			1	BT	c	a	S
	<i>Sphenodesme</i>	<i>triflora</i>	VR4	3	4			4	BO	e	s	NG
	<i>Teijsmanniodendron</i>	<i>simplicifolium</i>	VR2	3	2			2	DI	c	a	NG
Xanthophyllaceae	<i>Xanthophyllum</i>	sp.	XA1	E			1	1	BO	e	a	NG
Zingiberaceae	Genus unknown	sp.	ZI1	E			1	1				NF
Family, genus unknown		sp.1	U1	L			1	1				G
		sp.2	U2	E	1			1				A
		sp.3	U3	E	1			1				NF
		sp.4	U4	E	1			1				NG
		sp.5	U5	L	1			1				NG
		sp.6	U6	E	1			1				NG
		sp.7	U7	E	1			1				NF
		sp.8	U8	L	1			1				NG
		sp.9	U9	L	1			1				NF
		sp.10	U10	G	1			1				A
		sp.11	U11	G	1			1				S
Total					430	194	56	576				