

**PLANT REPRODUCTIVE PHENOLOGY OVER FOUR YEARS  
INCLUDING AN EPISODE OF GENERAL FLOWERING IN A  
LOWLAND DIPTEROCARP FOREST,  
SARAWAK, MALAYSIA<sup>1</sup>**

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The first systematic observation of a general flowering, a phenomenon unique to lowland mixed-dipterocarp forests in Southeast Asia, is presented. During general flowering, which occurs at irregular intervals of 3–10 yr, nearly all dipterocarp species together with species of other families come heavily into flower. We monitored reproductive phenology of 576 individual plants representing 305 species in 56 families in Sarawak, Malaysia. Observations continued for 53 mo from August 1992 and covered one episode of a general flowering cycle. Among 527 effective reproductive events during 43 mo, 57% were concentrated in the general flowering period (GFP) of 10 mo in 1996. We classified 257 species into flowering types based on timing and frequency of flowering. The most abundant type was “general flowering” (35%), which flowered only during GFP. The others were “supra-annual” (19%), “annual” (13%), and “sub-annual” (5%) types. 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. Possible causes for general flowering, such as promotion of pollination brought about by interspecific synchronization and paucity of climatic cues suitable for flowering trigger, are proposed, in addition to the predator satiation hypothesis of Janzen (1974).

**Key words:** Borneo; dipterocarp forest; flowering trigger; general flowering; Malaysia; predator satiation; promotion of pollination.

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 com-

petition, herbivory, pollination, and seed dispersal, in addition to various climatic variables (Brody, 1997; reviewed by Rathcke and Lacey, 1985; van Schaik, Terborgh, and Wright, 1993). It has been demonstrated for some plant species that reproductive success or mortality is correlated with 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 in 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 and Kodric-Brown, 1979; Poole and Rathcke, 1979; Wheelwright, 1985; Kochmer and Handel, 1986; Murray et al., 1987; Ollerton and Lack, 1992; Wright and Calderon, 1995; but see Pleasants, 1980; Gleeson, 1981; Armbruster, 1986; Ashton, Givnish, and Appanah, 1988). There is still little strong evidence of competition for pollinators among co-occurring species (but see Campbell, 1985; Campbell and Motten, 1985), and flowering may be completely out of phase with pollinator abundance (Zimmerman, Roubik, and Ackerman, 1989). On the other hand, some studies suggest that synchronized flowering of different species could facilitate pollination through increase of resource density and local

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pollinator attraction (Schemske, 1981; Thompson, 1982). There are many other possible mechanisms that reduce competition for pollinators yet do not involve divergence in flowering time (Ollerton and Lack, 1992). Kochmer and Handel (1986) and Wright and Calderon (1995) suggested that phylogenetic factors strongly affect flowering phenologies on a large scale.

In the temperate region, clear annual cycles in plant phenology predominate. Presumably, winter limits biological activities and molds such patterns. In contrast, in tropical regions, where seasonal fluctuation in mean temperature is often less than fluctuation within a single day, periodic change in rainfall caused by movements of the intertropical convergence zone (ITCZ) often determine seasonality (van Schaik, Terborgh, and Wright, 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 (Augspurger, 1981; Borchert, 1983; Reich and Borchert, 1984; Murali and Sukumar, 1994).

The central part in Southeast Asian tropics, however, lacks 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). The Dipterocarpaceae represent the major component among the canopy and 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 plants 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 and Appanah, 1980; Appanah, 1985, 1993; Ashton, 1989, 1993; Ashton, Givnish, and Appanah, 1988; Corlett, 1990). During general flowering, which occurs at irregular intervals of 3–10 yr, nearly all dipterocarp species, together with species of other families, come heavily into flower. Related species of dipterocarps may flower sequentially with high intraspecific synchrony (Appanah and 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. Although the phenomenon is sometimes referred to as "mass flowering," in this paper we use the term "general flowering" to distinguish it from phenomena, such as "masting" or "mast fruiting," which are shown by populations of a single species or closely related species (Kelly, 1994).

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 2°C in daily minimum temperature (Ashton, Givnish, and Appanah, 1988), or an increase in sunshine (Ng,

1977; van Schaik, 1986). Seed-predator satiation is thought to explain the interspecific mass-flowering event, which leads to mast fruiting (Janzen, 1974; Ashton, Givnish, and Appanah, 1988), while there are no data demonstrating predator satiation in the forests.

Although the importance and uniqueness of the general flowering phenomenon have been stressed by other authors (Ashton, 1969; Janzen, 1974; Appanah, 1985, 1993; Ashton, Givnish, and Appanah, 1988), there is no detailed study that accurately describes a general flowering at the community level or examines the prevalence of the phenomenon among species of different life form, pollination mode, or fruit dispersal mode. Records of gregarious flowering in most studies are restricted to the Dipterocarpaceae (Burgess, 1972; Ng, 1977; Yap, 1987; Yap and 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) and a much shorter period than one general flowering cycle (Corlett, 1990).

We monitored individuals of 576 individuals representing 305 plant species in 56 families in Lambir Hills National Park, Sarawak, Malaysia, from August 1992 to December 1996. At the beginning of our study, the forest was at the final stage of fruiting following a general flowering event in 1992. We observed general flowering for the first time in 1996. Thus, these phenology data comprise the first relatively complete documentation of a general flowering cycle.

Tree towers and aerial walkways constructed in the park in 1992 enabled us to accurately record phenology and reproductive activities of plants of various life forms (Inoue et al., 1995; Yumoto, Inoue, and Hamid, 1996), as well as to observe the reproductive ecology of individual species. To examine flowering patterns at the individual and population levels that comprise patterns found at the community level, we 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. In addition, the factors that promote and maintain general flowering were inferred in light of these detailed and systematic observations.

## MATERIALS AND METHODS

**Study site**—The study was carried out in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20' N, 113°50' E, 150–250 m above sea level). Rainfall data collected at Miri Airport, 20 km from the research site, for 30 yr show that monthly rainfall fluctuated greatly up to 800 mm, and annual rainfall ranges between 2100 and 3300 mm. Though a dryer period was observed from January to March 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) (Fig. 1).

Observation was made in the Canopy Biology Plot (8 ha: 200 × 400 m, Inoue et al., 1995) and a belt transect along the waterfall trail (5 ha: 1 km × 50 m). The Canopy Biology Plot included humult and udult soils (sandy clay, light clay, or heavy clay in texture), several ridges

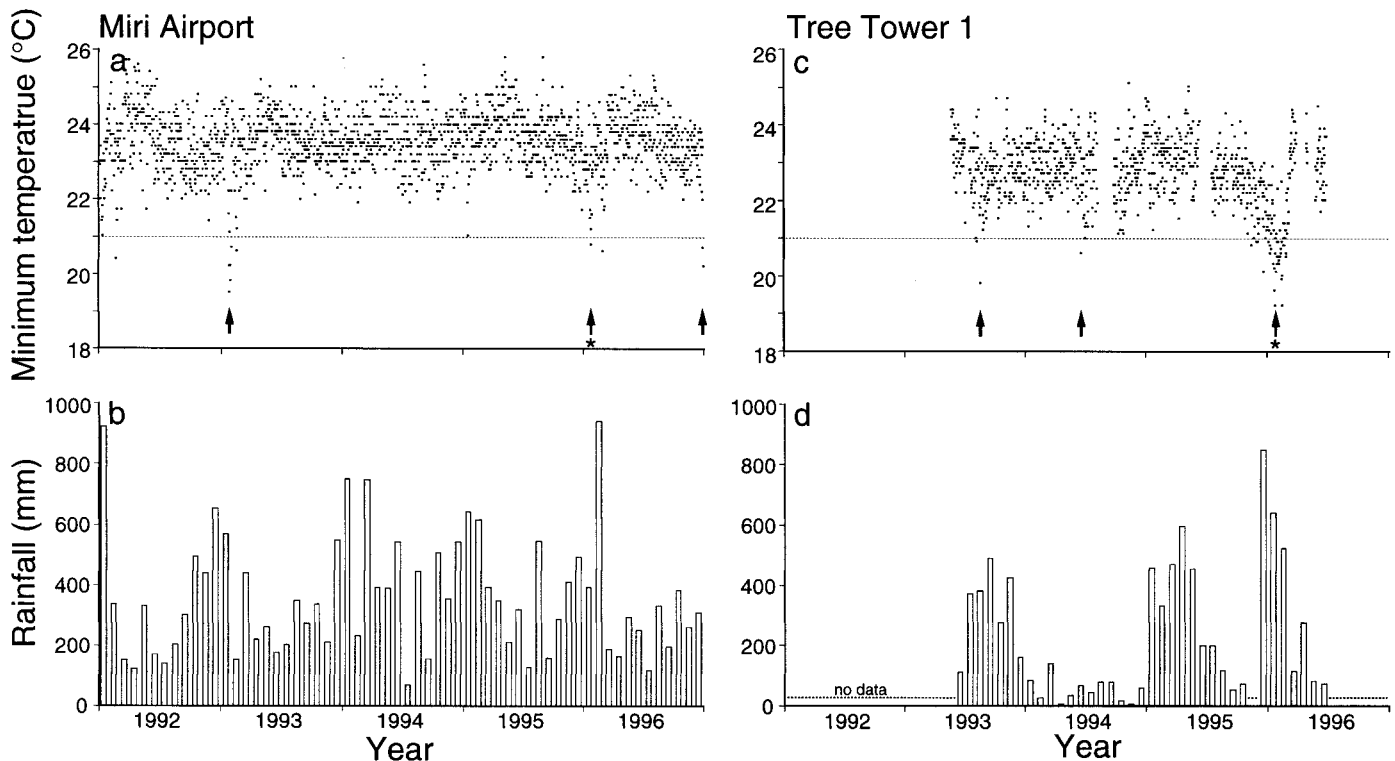


Fig. 1. Climate data at Miri Airport, located 20 km from Lambir National Park, and in the canopy at Lambir during the study, from 1992 to 1996. (a) Daily minimum temperature at Miri Airport. (b) Monthly rainfall (mm) at Miri Airport. (c) Daily minimum temperature in Lambir. (d) Monthly rainfall (mm) 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.

and valleys, and closed (mature-stage) forests and canopy gaps. In the mature part of this forest sample, closed canopy and subcanopy layers develop between 10 and 40 m above the ground. Above them, crowns of emergent trees sometimes stand out above 70 m. At the center of the Canopy Biology Plot, a canopy observation system (two tree towers, nine aerial walkways, and seven tree terraces) was constructed (Inoue et al., 1995; Yumoto, Inoue, and Hamid, 1996). The walkways penetrate the canopy or subcanopy layer. The waterfall trail is located along a stream on yellow sandstone, from the headquarters of the park to the Operation Raleigh Tower, which is another tree tower constructed by Operation Raleigh and donated to the park.

**Monitoring of climatic condition in the canopy**—We set meteorological sensors (rainfall: B-011-00; temperature/humidity: E7050-10; solar radiation: H-205) and a data logger (M-812-Z4 of Yakogawa Weatherac Corporation, Tokyo) on Tree Tower 1 in May 1993 (Yumoto, Inoue, and Hamid, 1996). 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-m 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. Our rainfall data from under the tree crown underestimate by ~34%, because part of the actual rainfall is caught by foliage of the tower tree extending over the device (Momose et al., 1994). We examined whether drops in daily minimum temperature could be a potential trigger for general flowering.

**Species and life-form types**—We chose 576 individual plants of 305 species in 56 families to reflect the various plant life forms in order to monitor phenology at the community level (Appendix). Our 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 emer-

gent trees), especially in the census from the forest floor. For the census from the tree towers and walkways, 430 trees were observed from the canopy access system and 56 from the Operation Raleigh Tower. In the census from the forest floor, all 194 plants were observed in the Canopy Biology Plot. One hundred and four plants were observed from both the forest floor and the canopy observation system.

We collected specimens of all accessible plants [all 194 individuals observed from the forest floor; 282 (58%) out of 486 individuals observed from the canopy observation system]. When the plant was flowering or fruiting, fertile specimens were collected and their floral characters (flowering time in a day, reward, color, and shape) were recorded. This collection of plant specimens (Plants of Sarawak, Canopy Biology Program) was identified in SAR (Sarawak Herbarium, Sarawak Forest Department). Specimens were sent to some herbaria, among which SAR and KYO (Herbarium, Kyoto University) have a complete set [see Nagamasu and Momose (1997) for details].

The plants were classified into eight life forms. Most tree species were distinguished by the height of the final developmental stage of reproductive individuals: forest floor (code = 1: maximum height <2.5 m), understory (2: 2.5–12.5 m), subcanopy (3: 12.5–27.5 m), canopy (4: 27.5–42.5 m), and emergent (5: >42.5 m). Forest floor plants were not included in this study. We dealt with tree species that grew only at newly made canopy gaps as gap trees (G) independently from the above five tree categories, regardless of their height. Other than trees, we distinguished epiphytes (E) and lianas (L). *Ficus* (Moraceae) species were not included in this classification, because all *Ficus* species has similar phenologies to maintain their pollinator populations, irrespective of their habits (see citations in table 1 of Bronstein et al., 1990; Milton, 1991).

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 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 six plant species) and insect pollinators were collected as far as possible by flower beating and net sweeping (for 93 plant species). 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 we could not observe or collect flower visitors, 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 species in this study and 172 species by general observations in the same study site).

This paper follows the categories of pollination systems reported by Momose et al. (1998b) except the “solitary” bee-pollinated group, which is further divided into four bee groups (*Xylocopa*, *Amegilla*, Halictidae, and *Megachile*) in Momose et al. (1998b). Ten pollination systems were distinguished in this study: (1) mammal pollination (obligately pollinated by mammals), (2) bird pollination (obligately pollinated by *Nectarinia jugularis*, *Arachnothera longirostra*, and *A. robusta* [Nectarinidae]), (3) *Apis* pollination (pollinated by *Apis dorsata*, *A. koschevnikovi*, and *A. andreniformis* [Apinae]), (4) small-social bee pollination (pollinated by *Trigona* spp. [Meliponini] or *Braunsapis* spp. [Allodapini], but several other insect families were also pollinators), (5) solitary bee pollination (obligately or dominantly pollinated by *Xylocopa* spp. [Xylocopini], *Amegilla* spp. [Anthophorini, Apidae], *Nomia* spp., *Thrinchostoma* spp. [Halictidae], or *Megachile* spp. [Megachilidae, Hymenoptera]), (6) fig wasp pollination (all *Ficus* spp.), (7) lepidopteran pollination (obligately pollinated by lepidopteras), (8) beetle pollination (obligately or predominantly pollinated by Chrysomelidae, Curculionidae, Nitidulidae, and Scarabaeidae), (9) diverse insect pollination (pollinated by several families or insect orders and not dominated by any), and (10) others (obligately or predominantly pollinated by thrips, flies, wasps, or cockroaches). The second most common pollination system, beetle pollination, was divided into two categories: beetle pollination found in the Dipterocarpaceae was distinguished from 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; Sakai et al., 1999).

Three fruit types were distinguished. The species producing fruits or seeds with special rewards for vertebrate vectors, such as sarcocarps, were distinguished as the animal-dispersed type. The other species were classified into two categories according to the dry mass 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 mass, whether they have some apparatus to disperse fruits (e.g., wing) or not. The dispersal distances of seeds with heavy mass 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 were classified as small fruit, since they are easily dispersed by wind and unlikely to suffer heavy predation from generalists. In this paper, we adopted the classification based on seed mass rather than seed morphology in order to examine the predator satiation hypothesis. If satiation of generalist pred-

ators is an important factor in general flowering, some differences in phenological strategies among fruit types are likely to be found.

**Observation and description of phenology**—From the canopy observation system, plant phenology was monitored twice a month from August 1992. This paper reports the results for 53 mo up until December 1996. All the individuals for the census from the canopy observation system had been fixed by July 1993, so that the reproductive phenology of 453 plants of 257 species were recorded for at least 43 mo. Among the 257 species, 68% of the species were represented by a single individual, and 16 and 7% by two and three, respectively. Nine percent of species included more than three individuals. Data taken during the 10 mo before selection of all individuals for the census were only used in analyses of overall patterns of flowering and fruiting (see Fig. 2) and fruit set data (see Table 3). From April to July 1996 the census was intensified to three times a month for higher accuracy over the general flowering period.

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. Intensity of plant reproductive activities in each census was 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 flowers was defined to be “flowering,” and the plant with any mature or immature fruits was “fruiting.”

Among 486 plants observed from the canopy observation system, 11 individuals were excluded from analyses because their reproductive structures were sometimes confused with their leaves. For all the 22 individuals of Moraceae and seven individuals of other families, distinction among flower buds, flowers, immature and mature fruits was sometimes difficult because their flowers and fruits were similar in shape and/or color (e.g., syconia of *Ficus*). Data of these individuals were excluded when distinction between flowers and fruits was important (see Figs. 2, 5–8; Table 3). Individuals that died during the census (22 individuals) were excluded from the analyses.

The census from the forest floor 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 the forest floor and from the canopy observation system, we referred to the records of the previous census 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. We also censused leaf flushing simultaneously with reproductive phenology, but will report these results in another paper.

**Description of reproductive events**—For each reproductive event, the first, peak, and last observation dates of flowering were recorded. 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, we used the last census date. Observation dates of fruiting were also recorded in the same manner as flowering. 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 the number of days between the first and last dates of flowering. If flowering was observed only once, the 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. The flowering length of each plant category

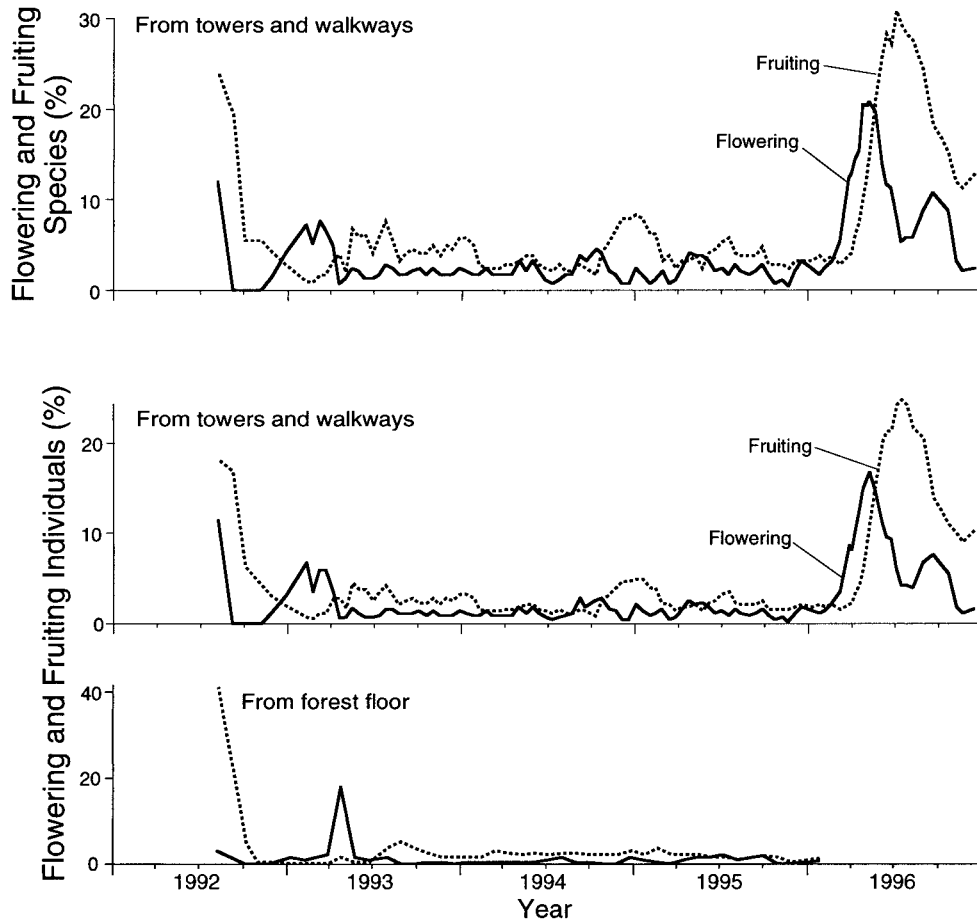


Fig. 2. Changes in the percentage of flowering and fruiting species and individuals observed from the forest floor (190 individuals) and the tree towers and walkways (237 species, 428 individuals).

was compared with that of the other species by the Wilcoxon two-sample test (two-tailed).

Magnitudes of the flowering, fruiting, and whole reproductive event were determined to be the maximum grade of intensity of plant reproductive activities defined above through the period with flowers, mature fruits, and the whole episode, respectively. 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 mo from June 1992 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” independent of the number of the events during GFP. All other individuals were classified based on flowering frequency. When the frequency was five or more, 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 type, we 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-an-

nual, 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 categorize the species that did not reproduce during the study into “nonflowering,” tentatively.

We examined correlations between the proportions of general flowering species and the plant categories (life-form types, pollination systems, and fruit types) by  $\chi^2$  tests. Species that we observed reproducing at least once during the 43 mo and plant categories with >15 species were included in the analyses because the test requires expected frequencies  $\geq 5$  (Sokal and Rohlf, 1981).

**Statistical tests for temporal distribution of reproductive events**—In the first place, we performed two analyses to evaluate temporal concentration of flowering events in general flowering: calculation of an index of aggregation, and a statistical test to examine whether the observed distribution of flowering events significantly deviated from random distribution. In the first analysis, we calculate Morisita’s Index,  $I_d$ , an index of aggregation independent of sample size, based on temporal distribution of effective reproductive events in 14 3-mo periods from July 1993 to December 1996. 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 other analysis, the  $\chi^2$  test for goodness of fit, was performed assuming that flowering events occurred at random throughout the 14 3-mo periods (when the sample size was  $\geq 70$ ) or 7 6-mo periods (when

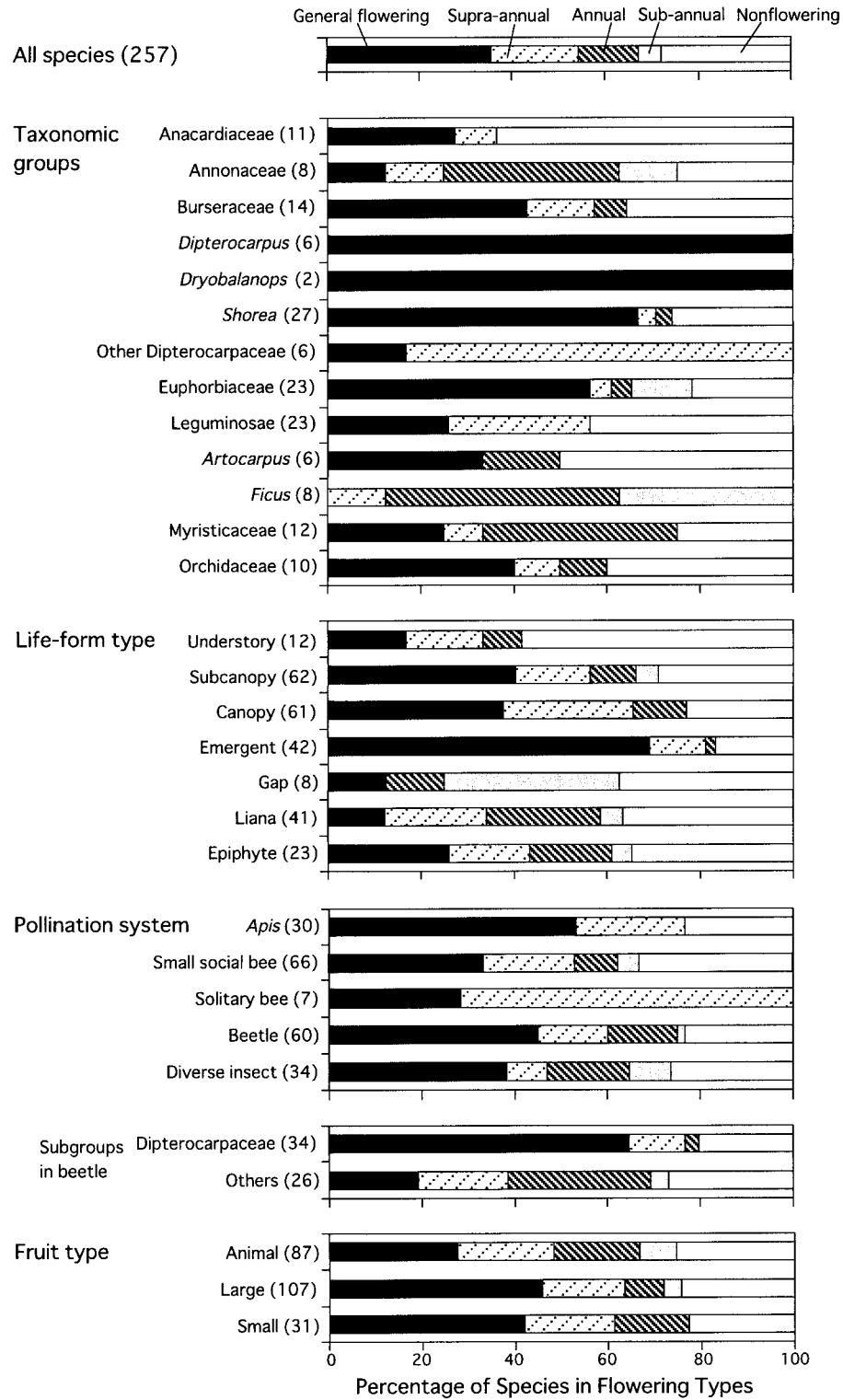


Fig. 3. The proportions of the four flowering types (sub-annual, annual, supra-annual, and general flowering) and nonflowering species (species not flowering during the study) among all species observed, taxonomic groups, life-form types, pollination systems, and fruit types. Pollination systems with less than five species were not included. Numbers of species included are shown in parentheses.

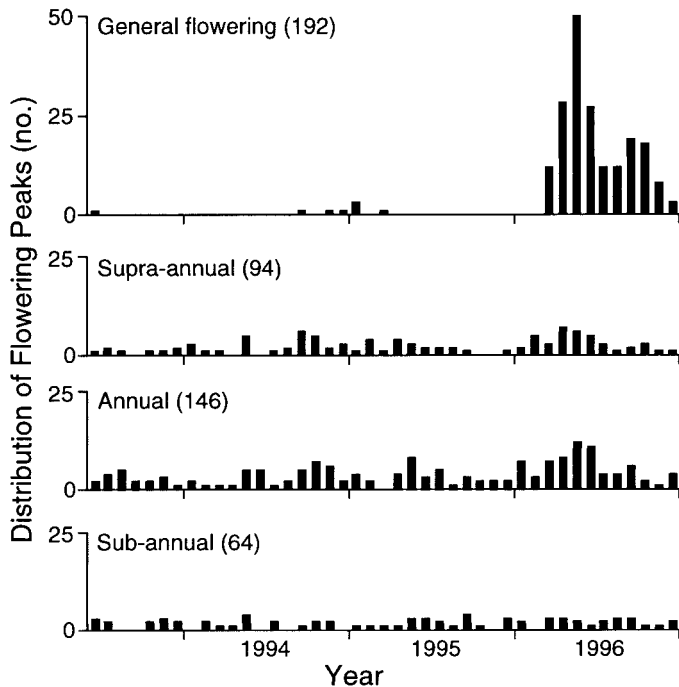


Fig. 4. Temporal distribution of effective flowering peaks in each month in the four flowering types. The numbers of the reproductive events included in the data are shown in parentheses.

35  $\leq$  sample size <70) from June 1993. The test was not performed for the plant categories with flowering events <35, because the test requires expected frequencies  $\geq 5$  (Sokal and Rohlf, 1981), which means that the expected numbers of flowering events in a unit period (3 or 6 mo) must be five or more. The two analyses were conducted for all the species and by plant categories (taxonomic groups, life-form types, pollination systems, and fruit types). In addition, interspecific aggregation of reproductive events was examined with the  $\chi^2$  test for goodness of fit assuming that the numbers of reproductive species in 3-mo periods were distributed at random.

Secondly, we compared flowering patterns of plants in the four flowering types we defined above. If plants of different flowering types respond to a different climatic cue for flowering, their flowering patterns must be different and have no correlations with each other. We examined correlations of the numbers of the effective reproductive events in every 3-mo period between flowering types by Spearman's rank correlation test.

Finally, fruit set (the proportions of effective flowering events resulting in effective fruiting) during non-GFP and GFP was compared by flowering types. If there are differences in factors related to fruit set between GFP and non-GFP, the differences may explain evolution of general flowering. Statistical significance of the difference in fruit set between GFP and non-GFP was examined by Fisher's exact test (one-tailed).

## RESULTS

**Climatic conditions**—Drops of daily minimum temperature to  $<21^\circ\text{C}$  at Miri Airport were observed three times during the study period: January–February 1993 for 6 d; January–February 1995 for 2 d; and December 1996 for 2 d. Drops at Lambir Hills National Park were also recorded three times during periods of observation: August 1993 for 3 d; June 1994 for 1 d; and November 1995–February 1996 for 30 d (Fig. 1). The drop in De-

cember 1996 in Lambir was very strong, continuing from 14 November 1995 to 27 February 1996, with the lowest temperature being  $19.2^\circ\text{C}$ . 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 sites, yearly and monthly fluctuation patterns were quite different. Lambir experienced drought in 1994, when average monthly precipitation was about one-fifth of a normal year. However, the total precipitation at Miri Airport in 1994 was the highest in the 5-yr period, 1992–1996 (Fig. 1). 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**—Seventy-four percent of 486 individuals in the census from the canopy observation system and 98% of 194 individuals in the census from the forest floor were non-gap trees. The emergent layer was dominated by Dipterocarpaceae (73% of 48 species). In the lower layers, Anacardiaceae, Burseraceae, Euphorbiaceae, and Myristicaceae were the most common families, but no one family dominated. Most lianas belonged to Leguminosae (24% out of 45 species) and Annonaceae (seven species). Epiphytes included 14 species of Orchidaceae, three species of Loranthaceae, and two species 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. In the lower layers, small social bees, diverse insects, and non-dipterocarp beetle pollinators predominated. Non-dipterocarp beetle pollination was found most often in Annonaceae and Myristicaceae, which occupy lower layers or are lianas. The plants pollinated by diverse insects and small social bees belonged to various families. Most of the gap trees were pollinated by small social bees (seven out of nine species). Among 45 liana species, eight species were beetle-pollinated Annonaceae. In general, long-distance pollinators such as mammals, birds, solitary bees, and lepidopterans played limited roles (Appendix).

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

**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 the canopy observation sys-

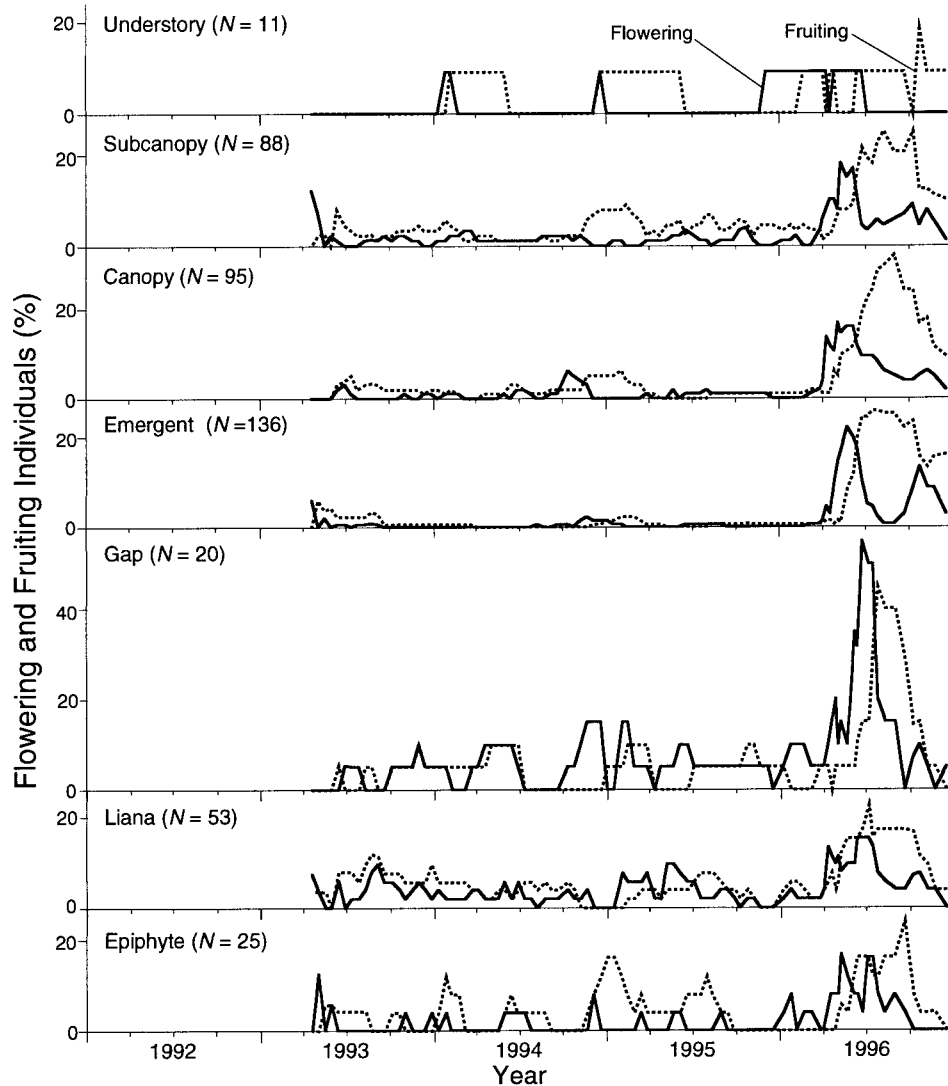


Fig. 5. Changes in percentage of flowering and fruiting individuals of seven plant life-form types. Numbers of individuals observed are shown in parentheses.

tem and from the forest floor (Fig. 2). Observations from the canopy observation system revealed that percentage of flowering individuals was low during non-GFP, usually <3.0% with a minor peak up to 6.7% in the first quarter of 1993. A minor increase of flowering individuals was recorded by the census from the forest floor in April 1993 (Fig. 2). Among 33 individuals flowering at that time, 16 were Dipterocarpaceae, including two species of *Dryobalanops*, *Dipterocarpus pachyphyllus*, and seven species of *Shorea*, though their intensities of reproduction were not recorded during this preliminary census period. The plants observed from the canopy observation system did not show such a clear increase, but a small peak was detected in February and March. Reproductive events of seven dipterocarp species with a magnitude “+” were found from the canopy observation system in February and March 1993.

The proportions of flowering species and individuals increased drastically in March 1996 and reached 21.1 and 16.9%, respectively, in May 1996. A lower flowering

peak was observed in October 1996, half a year after the first peak. Although a fruiting peak corresponding to the latter flowering peak did not appear in Fig. 2, it was observed at the beginning of 1997 (Sakai, unpublished data). We 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 GFP, 202 effective reproductive events of 129 species and 99 events of 69 species were recorded, respectively.

General flowering started 1–2 mo after a drop in minimum temperature observed at Lambir from December 1995 to February 1996, with the lowest temperature being 19.2°C (Figs. 1, 2). Though two other minor drops to <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 we did not collect meteorological data at that time.

In total, 664 reproductive events of 453 plants, includ-



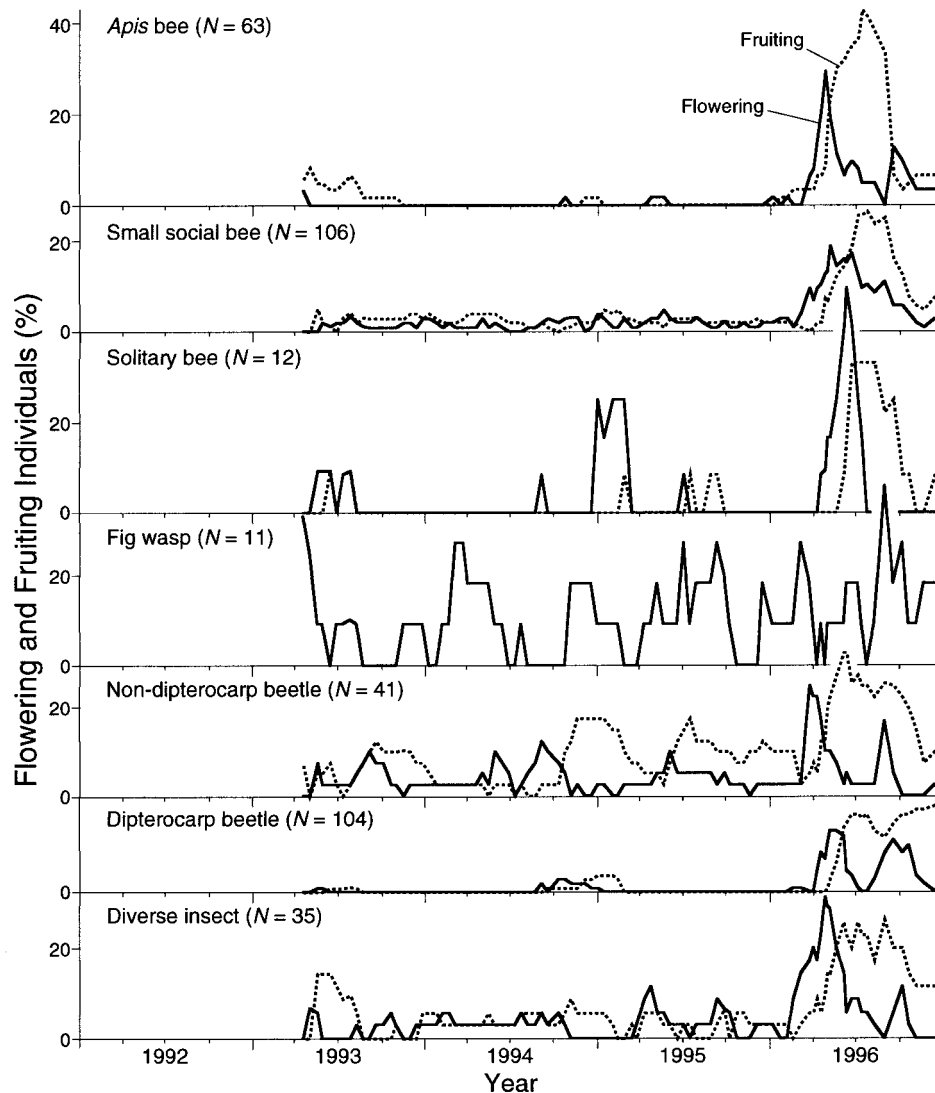


Fig. 6. Changes in percentage of flowering and fruiting individuals of seven pollination systems. Numbers of individuals observed are shown in parentheses. In the fig-wasp pollination system, the percentage of individuals that have syconia is shown.

ing 527 effective reproductive events, were recorded during the 43 mo (Table 1). More than one-third (163 individuals) of the individuals reproduced only once, and about the same number of individuals (164) did not flower during the 43 mo. Fifty-seven percent out of the 527 effective events were concentrated during GFP, especially in the 3 mo from April to June 1996 (30%, 160 events). Both the reproductive events and the number of species reproducing in every 3-mo 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 mo, and 61% of them flowered once or more during GFP.

**Flowering types**—The most abundant flowering type among the 257 species was general flowering (35%), followed by supra-annual (19%), annual (13%), and sub-annual (5%) (Table 2; Fig. 3). Effective reproductive events were not observed for 72 species (28%) through-

out the 43 mo. Among the general flowering species, the maximum number of reproductive events of an individual was recorded by *Bouea* sp. 2 (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) we observed flowered only once or twice during the 43 mo.

In comparisons among taxonomic groups, general flowering species dominated in *Dryobalanops*, *Dipterocarpus*, *Shorea* (Dipterocarpaceae), Euphorbiaceae, Burseraceae, and Orchidaceae (Fig. 3). The other dipterocarp species, including *Cotylelobium* (one species), *Hopea* (one species), *Parashorea* (one species), *Vatica* (three species), were categorized into the 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 Myris-

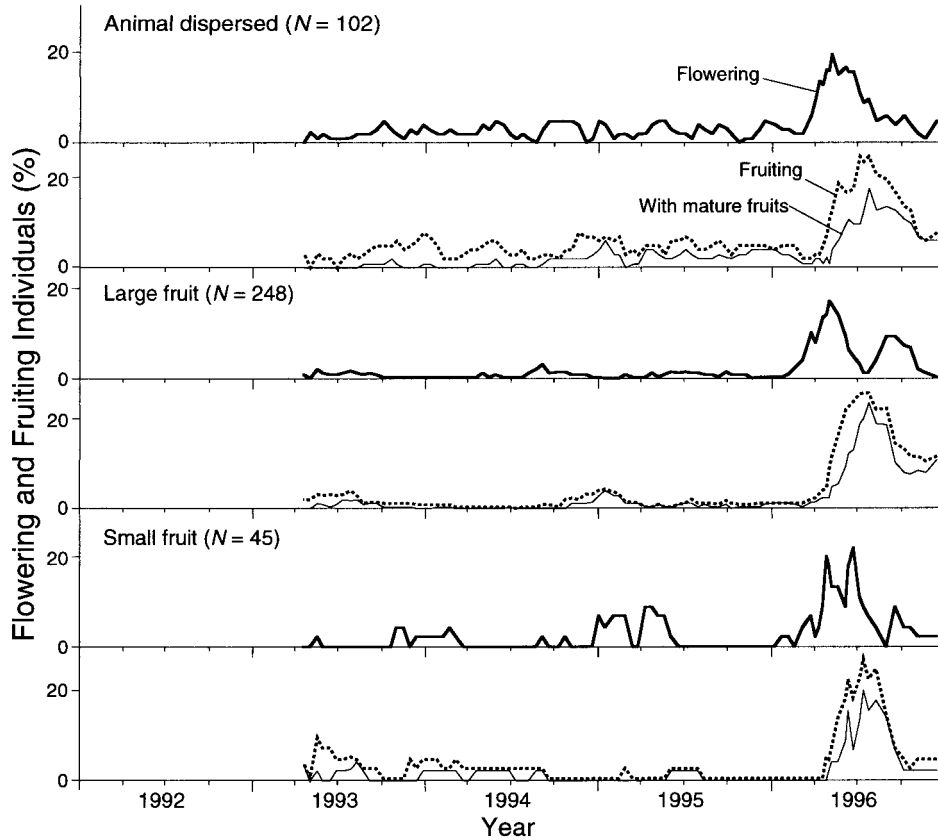


Fig. 7. Changes in percentage of flowering and fruiting individuals of three fruit types. Numbers of individuals observed are shown in parentheses.

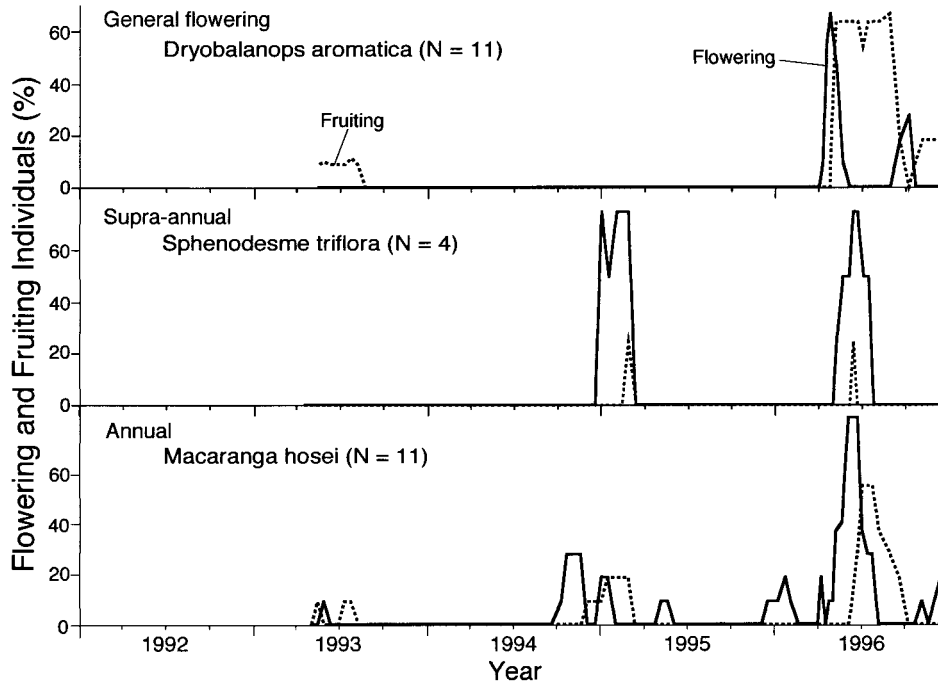


Fig. 8. Changes in percentage of flowering and fruiting individuals of three species (*Dryobalanops aromatica* [Dipterocarpaceae], *Sphenodesme triflora* [Verbenaceae], and *Macaranga hosei* [Euphorbiaceae]) of different flowering types. Numbers of individuals observed are shown in parentheses.

TABLE 1. Temporal distribution of reproductive events recorded for 524 individuals monitored from a canopy observation system (TW) for 43 mo.

Year	Quarter <sup>a</sup>	Magnitude of reproductive event <sup>b</sup>				Sum of 1-3	Total	No. of species
		+	1	2	3			
1993	June <sup>c</sup>	5		7		7	12	7
	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
1995	4	10	7	17	7	31	41	26
	1	4	3	7	9	19	23	14
	2	2	7	13	11	31	33	26
1996	3	6	7	7	7	21	27	20
	4	1	3	6	2	11	12	10
	1	2	12	15	17	44	46	35
1996	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	

<sup>a</sup> 1, January–March; 2, April–June; 3, July–September; 4, October–December.

<sup>b</sup> + = 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.

<sup>c</sup> Start of study.

ticaceae. More than 44% of Anacardiaceae, Leguminosae, and *Artocarpus* (Moraceae) did not reproduce during the study period.

Results of  $\chi^2$  tests for goodness of fit to random distribution of reproductive events strongly indicated that reproductive events of Dipterocarpaceae and *Shorea*, Euphorbiaceae and Leguminosae were significantly concentrated ( $P < 0.001$ , Table 2). The most strong aggregations were exhibited by *Artocarpus* ( $I_d = 9.3$ ), *Dipterocarpus* ( $I_d = 8.4$ ), *Dryobalanops* ( $I_d = 7.6$ ), and Burseraceae ( $I_d = 4.6$ ), though statistical significance of their aggregation could not be examined due to the small sample size. On the other hand, the events of *Ficus* did not show aggregation ( $I_d = 0.92$ ) (Table 2).

In the general-flowering type, 97% of 182 effective flowering events were observed during GFP and 54% from April to June (Fig. 4). Figure 4 shows that plants of the general-flowering type flowered even during non-GFP in spite of the definition of general-flowering type. It is due to majority rule in the definition: if the larger part of the population flowers only in GFP, the species is categorized into the general-flowering type despite flowering of the small part of the population in non-GFP. The same or different individuals of 27% of 91 general-flowering species reproduced during both the first and second GFP.

The percentage of flowering events during GFP was much less in the other flowering types: 35% of 83 events of the supra-annual; 37% of 117 events of the annual; and 33% of 46 events of the sub-annual type. Nearly one-half of supra-annual species (23 species out of 48 species) reproduced during GFP, and the average number of flowering events per month per individual was higher during the GFP than during non-GFP (0.052 and 0.032 events·mo<sup>-1</sup>·individual<sup>-1</sup> for GFP and for non-GFP, re-

spectively). The difference was larger in the annual-flowering type (0.107 for GFP and 0.056 for non-GFP). The same tendency was found in sub-annual species (0.175 for GFP and 0.126 for non-GFP).

Positive correlations in temporal distributions of flowering peaks were found between flowering types (Fig. 4). The strongest correlation was detected between annual and supra-annual types (Spearman's correlation coefficient:  $r_s = 0.62$ ,  $P = 0.019$ ). The correlations between general flowering and supra-annual types and between general flowering and annual types were also significant ( $r_s = 0.59$ ,  $P = 0.028$  and  $r_s = 0.54$ ,  $P = 0.045$ , 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). The difference was the largest in general-flowering type. Fisher's exact tests detected significant differences in general flowering and annual types ( $P = 0.037$  in general flowering and  $P = 0.036$  in annual). On the other hand, fruit set was not significantly different in sub-annual or supra-annual species.

**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. 5). Half of 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 the general-flowering type was significantly different among life-form types that included >15 species (subcanopy, canopy, emergent, liana, epiphyte) ( $P < 0.001$ ). The proportion was the highest in the emergent type (69%) (Table 2; Fig. 3). 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, 12, and 26%, respectively). More than half of the species (seven out of 11 species) 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 2). In mature forest larger  $I_d$  was found in the higher strata ( $I_d = 3.8, 2.7, 2.3$ , and 1.6 for emergent, canopy, subcanopy, and understory, respectively; Table 2).  $I_d$  of gap-type trees (1.5) was smaller than non-gap trees. Lianas and epiphytes exhibited less aggregation ( $I_d = 1.2$  for both liana and epiphyte).

**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. 6). On the other hand, a small proportion of individuals pollinated by small social bees, non-dipterocarp beetles, or diverse insects flowered one after another, so that they continuously flowered at the community level during non-GFP

TABLE 2. Number of species in taxonomic groups, life-form types, pollination systems, fruit types, by flowering types. Results of  $\chi^2$  test for goodness of fit (one-sided) assuming that their flowering events occurred at random throughout the 14 3-mo periods from July 1993 (when the number of reproductive events  $\geq 70$ ) or seven 6-mo periods (when  $< 70$  and  $> 34$ ) are shown.

	Flowering type						No. of individuals <sup>a</sup>	No. of events	$I_d$	$\chi^2$ test for goodness of fit <sup>b</sup>
	Nonflowering	General flowering	Supra-annual	Annual	Sub-annual	All				
Total (%)	72 28.0	91 35.4	48 18.7	34 13.2	12 4.7	257 100.0	453 (289)	522	1.98	***
Taxonomic group										
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)	40	1.06	—
Myristicaceae	3	3	1	5		12	16 (11)	30	1.51	—
Orchidaceae	4	4	1	1		10	10 (6)	9	2.72	—
Others	25	26	27	17	5	100	137 (97)	171	—	—
Life-form type										
Understory	7	2	2	1		12	12 (5)	10	1.56	—
Subcanopy	18	25	10	6	3	62	88 (55)	105	2.34	***
Canopy	14	23	17	7		61	105 (68)	104	2.66	***
Emergent	7	29	5	1		42	136 (86)	110	3.82	***
Gap	3	1		1	3	8	20 (15)	48	1.48	***
Liana	15	5	9	10	2	41	56 (34)	74	1.24	**
Epiphyte	8	6	4	4	1	23	25 (17)	35	1.25	ns
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	—
Beetle (C)	14	27	9	9	1	60	145 (85)	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	ns
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	—	—
Fruit type										
Animal dispersed	22	24	18	16	7	87	121 (88)	201	1.49	***
Large fruit	26	49	19	9	4	107	254 (153)	235	2.62	***
Small fruit	8	13	6	5	0	31	45 (32)	52	2.29	***

<sup>a</sup> The numbers except for individuals without flowering records are shown in parentheses.

<sup>b</sup> ns, not significant; \*\*,  $P < 0.01$ ; \*\*\*,  $P \leq 0.001$ ; —, not examined because of small sample size.

(Fig. 6). The proportion of flowering individuals in these plants became higher during GFP. Solitary-bee-pollinated plants exhibited sporadic reproduction (Fig. 6). *Ficus* had a unique flowering phenology and recorded a rather high percentage of reproducing plants continuously throughout the year. Their reproduction did not exhibit a significant difference from random distribution (Table 2).

The proportion of the general-flowering type was significantly different among pollination systems including  $> 15$  species (*Apis*, small social bees, non-dipterocarp beetles, dipterocarp beetles, diverse insects) ( $P = 0.002$ ).

A higher proportion of the general-flowering type was associated with *Apis* (53% out of 50 species) and beetles (45% out of 60 species) (Table 2; Fig. 3). In beetle systems, the percentage in Dipterocarpaceae (64% out of 34 species) was higher than that in other species (19% out of 26 species). Fig-wasp-pollinated *Ficus* (eight species) did not include any general-flowering species. The other pollination systems had 25–38% of general-flowering species. Two lepidopteran-pollinated species, *Dipterocarpus pachyphyllus* (Dipterocarpaceae) and *Barringtonia curranii* (Lecythidaceae), were of the general-flowering

TABLE 3. Comparison of fruit set during GFP and non-GFP. The proportions of effective flowerings that 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	None-GFP		GFP		$P$
	%	$N$	%	$N$	
General flowering	30.0	10	63.8	174	0.037*
Supra-annual	25.5	47	46.4	28	ns
Annual	32.8	67	52.5	40	0.036*
Sub-annual	23.1	26	15.4	13	ns

\*  $P \leq 0.05$ ; ns, not significant.

type. Reproductive events clumped significantly in *Apis*, small social bees, dipterocarp beetles, and diverse insect pollination systems, but not in the non-dipterocarp beetle-pollinated species. A relatively large  $I_d$  was found in lepidopteran (5.0), *Apis* (4.7), and dipterocarp beetle (3.5) pollination systems (Table 2).

**Flowering patterns of fruit types**—All three fruit types showed a drastic increase of flowering and fruiting individuals during GFP (Fig. 7). Only large-fruit species unambiguously showed the two-peaked flowering pattern. Changes in the proportion of individuals with mature fruits followed those of flowering ~3 mo before. Sharpness of flowering and fruiting peaks, i.e., strength of temporal aggregation of flowering and fruiting, differed little among the three fruit types. During non-GFP, large-fruit species including dipterocarps exhibited less reproduction than the other species.

The proportion of the 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 types (Fig. 3). Distribution of flowering events was significantly aggregated in all fruiting systems. The largest  $I_d$ , found in the large-fruit type, was mainly due to that type having few reproductive events during non-GFP (Table 2).

**Flowering patterns at the population level**—Flowering and fruiting patterns of three species, classified in different flowering types, were examined at the population level (Fig. 8). They 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. 8). Among 11 individuals, seven and three 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 four individuals that we observed flowered at the beginning of 1995, and three reproduced again during GFP. A gap tree, *Macaranga hosei* (Euphorbiaceae), reproduced rather frequently and showed annual flowering. Flowering was synchronized among individuals, but the flowering intervals were irregular (Fig. 8). Only a few trees of the species participated in each flowering event during non-GFP, while up to nine 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 showed flowering patterns 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.

**Length of flowering period**—The four flowering types, taxonomic groups, life-form types, and pollination systems did not show a significant difference in the length of flowering period from the rest of the species. Gap species had the longest flowering period. The species flowering longer than 120 d were the liana *Artabotrys venustus* (Annonaceae), the canopy tree *Coelosetgia griffithii* (Bombacaceae), and the subcanopy tree *Vernonia arborea* (Compositae). The former two species were pollinated by beetles and the latter by *Apis*.

## DISCUSSION

**General patterns**—One cycle of the general-flowering phenomenon was recorded in the lowland mixed-dipterocarp forest in Lambir. 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. This paper is the first report to document plant reproductive phenology at the community level covering almost a complete cycle from one general flowering to another.

Although this study revealed some important characteristics of the general-flowering phenomenon, many species are represented by a single individual in this study, and further data are needed to discuss flowering patterns of individual species. We did not select species with large number of individuals, because the primary purpose of the study was to elucidate patterns at the community level, and we thought exclusion of rare species from samples could lead us to incorrect conclusions in studies of tropical forests with extremely high species diversity.

General flowering is a phenomenon at the community level, involving many plant species from many families. When the temporal distribution of flowering was examined by plant categories (taxonomic groups and life form, pollination, and fruit types) using  $I_d$  and  $\chi^2$  tests, most showed statistically significant aggregation. General-flowering species were found in various plant categories. The general-flowering phenomenon, a drastic increase of reproductive activity during a restricted period with low activity in intervening periods, is fairly prevalent in many plant groups. In addition, not only the general-flowering type but all flowering types have higher levels of reproduction during GFP.

The percentage of plants in flower during non-GFP was usually quite low in Lambir, compared with other tropical regions. In a lowland forest of La Selva, Costa Rica, 9–30% of overstory trees and 17–30% of under-story trees in a wet forest and 9–30% of tree species in a dry forest may flower all year (Frankie, Baker, and Opler, 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 pre-montane forest in Rwanda, 10–50% of tree species were flowering 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 >10% and sometimes exceeded 60% (Murali and Sukumar, 1994). In contrast, Medway (1972) reported similar figures to those of Lambir from a lowland dipterocarp forest in Peninsular Malaya. In most months 0–7% of species were flowering, while at most 35% of the species bloomed during GFP.

The low percentage of flowering individuals was mainly due to low flowering frequency or longer intervals between reproduction episodes of individuals. More than half of the species we observed were supra-annual or general-flowering species with a flowering interval longer than 1 yr. 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 yr) 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, Frankie, and Baker, 1994; Newstrom et al., 1994).

It is interesting that many plants that are domesticated for their edible fruits (e.g., *Parkia* [Leguminosae] and *Artocarpus* [Moraceae]) and are often found in local markets both in GFP and in non-GFP are categorized as general-flowering species in this study. The differences in reproductive intervals between wild plants and domesticated plants are probably not based on genetics but due to differences in their environments, such as light and nutrient conditions. Plants under cultivation reproduce more frequently than those in a natural forest, even if the plant is originally a general-flowering species.

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 did not flower during the study period. 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 the flowering intervals of 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, while the number of the social pollinators per flower is constant irrespective of display size. 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. By contrast, the canopy or subcanopy trees cannot wait as long between reproductive episodes because of higher mortality. For these trees it is optimal to frequently produce smaller displays 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, except for plants pollinated by *Apis dorsata*, a social bee species, which responds only to extraordinarily large floral resources and is closely associated with general flowerings as discussed below.

The observed patterns suggest 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. Moreover, 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 for flower induction. Differences in their flowering frequencies may reflect variation of the threshold values among species. Supra-annual and annual species reproduced during non-GFP not because they escape flowering during GFP, but because they have higher thresholds to induce flowering than that of general-flowering species. On the other hand, a small proportion of individuals classified as the general-flowering type also flowered during non-GFP. This agrees with a study by Yap and Chan (1990), which reports the existence of an intermediate intensity of flowering in addition to gregarious flowering in several species of *Shorea* (Dipterocarpaceae), representatives of general-flowering species. General-flowering species and others showed different flowering patterns, not because they have different mechanisms for flower synchronization but because they have different flowering frequency.

Coincidence of a flowering trigger can be explained by paucity of possible flowering in aseasonal forests. Synchronization within a species is quite important, particularly for outcrossing species with low density, to assure cross-pollination. The flowering trigger should be distinctive and reliable to ensure that individuals in various microhabitats sense it equally and exactly at the same time and that the switch is turned on at appropriate intervals. In the aseasonal tropical region of Lambir, possible climatic cues may be strictly limited and the plants may adopt the same environmental variable as a flowering trigger. That explains correlations in temporal distributions of flowering events observed among general-flowering, supra-annual, and annual flowering types. Contrarily, the existence of distinctive climatic cues with a 1-yr cycle may account for dominance of the annual pattern in other tropical regions.

**Trigger of general flowering**—Then, what is the trigger for general flowering? Ashton, Givnish, and Appanah (1988) investigated the environmental cue for floral induction and general flowering using 11 yr of meteorological

logical data and concluded that the most likely cue was a drop in daily minimum temperature by  $\sim 2^{\circ}\text{C}$ . Our data monitoring climatic conditions recorded a drop in minimum temperature by up to  $3^{\circ}\text{C}$  1–2 mo before a general flowering began and thus support this hypothesis.

The association of general flowering and El Niño Southern Oscillation is still controversial. Ashton, Givnish, and Appanah (1988) showed a correlation between general flowering and El Niño and suggested that drops of temperature were caused by radiative cooling associated with El Niño events, which bring about a continuous dry period. However, when general flowering started in Lambir and Peninsular Malaysia in 1996, it was rather a La Niña condition according to Southern Oscillation Index, the normalized value of the surface air pressure difference between Darwin and Tahiti. Considering the time lags from the flowering trigger to fruiting, contrary to the results of previous study (Ashton, Givnish, and Appanah, 1988), general flowering tends to be induced in normal to La Niña phases in Peninsular Malaysia (Yasuda et al., 1999). On the other hand, general flowering events in Sarawak occurred both in El Niño and La Niña years, and no simple association was found (Yoshida, 1998). In addition, the general flowering year does not always coincide even within Sarawak. Dipterocarp forests in north-eastern Sarawak including Lambir and in the southwestern part around Kuching exhibit different fruiting behaviors. Climatological mechanisms for a flowering cue may be different among years.

Van Schaik (1986) indicated that general flowering had an association with hours of sunshine. It is a reasonable idea that plants are responding to the relief of resource limitation by an increase in solar radiation in cloudless years, and mast fruiting events synchronize among species. Nevertheless, an increase in solar radiation was not observed in winter 1995/1996 in Lambir (Sakai et al., 1997) or in Pasoh forests, Peninsular Malaysia (Yasuda et al., 1999).

**Pollinators**—Differences among pollination systems in flowering patterns may be related to characteristics of their pollinators. Three tactics enable consumers of floral resources to respond 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 *Apis dorsata*. The seasonal migration of *A. dorsata* over 100 km between montane and lowland areas reported from Sri Lanka (Koeniger and Koeniger, 1980) demonstrates their ability to migrate a long distance. Around the 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 not last more than a year in the forest. The bees may adapt to great fluctuation in resource availability caused by general flowering by immigration rather than by storing resource.

Stingless bees are resident bees in Lambir (Nagamitsu and 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, and thus 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 (Inoue et al., 1984b, 1990, 1993; Salamah, Inoue, and Sakagami, 1990), which can quickly start foraging in response to an abrupt increase of ephemeral and massive floral resources in both GFP and non-GFP.

Differences in flowering patterns between these two bee-pollination systems, *Apis* pollination and small social-bee pollination, can be explained by the migrating and resident habit of the two kinds of bees. It is impossible for plants flowering during non-GFP to be pollinated by *A. dorsata* because the population density of *A. dorsata* is extremely low during non-GFP. The tight relationship among general flowering, *Apis* bees, and *Apis*-pollinated plants possibly has 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. Dominance by highly socialized bees including the genus *Apis* among pollinators, compared 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 due to the general-flowering phenomenon (Bawa et al., 1985; Kress and Beach, 1994; Momose et al., 1998b).

A feeding niche shift was found in beetle pollinators of Dipterocarpaceae. Some beetles pollinating Dipterocarpaceae are herbivores feeding on new leaves of dipterocarp trees during non-GFP without dipterocarp flowers (Sakai et al., 1999; M. Yamauti, unpublished data). An increase of floral resources might cause their feeding niche shift.

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 their host flowers, and their population is not maintained if flowering of their hosts occurs at irregular and long intervals. The proportion of general-flowering species in the Annonaceae, in which most members have highly specialized association with beetle pollinators (Gottsberger, 1989a, b), was the smallest of all the taxonomic groups that we examined except for *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 we examined, *Ficus* was unique in that no species belongs 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 and Eisikowitch, 1968; Compton, Wiebes, and Berg,

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).

One of possible ultimate causes for general flowering may be higher pollination success in GFP than non-GFP. The idea is supported by higher fruit sets in GFP than non-GFP found in general flowering and annual flowering species. Similar results are reported by Yap and Chan (1990) in several species of Dipterocarpaceae. Only recently have the prevalence and importance of outcrossing even in tropical forests with high species richness and low population densities of most plant species become recognized (Gan, Robertson, and Ashton, 1977; Hamrick and Murawski, 1990). In most tropical plants, outcrossing is achieved by animal pollen vectors (Bawa et al., 1985; Kress and Beach, 1994; Momose et al., 1998b). Aggregated flowering of various species sharing common pollinators may activate pollinators and result in higher pollination success than isolated flowering: an increase of floral resources 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. 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 exploited by stingless bees and thus contribute to the population growth of stingless bees even though the bees do not contribute to 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.

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 the Annonaceae and beetle pollinators also have a species-specific association. In such specific pollination systems where 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.

**Seed dispersal vectors and predators**—Janzen (1974) was apparently the first to evaluate ultimate causes of general flowering. He suggested that seed predators or herbivores, especially mammals and birds, which have general diets of fruits and seeds of a variety of species, could be the primary selective factor for synchronized flowering and fruiting of a variety of species. 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).

Our observations indicate that satiation of generalist predators alone cannot explain general flowering at the community level. First, considerable numbers of species in all fruit types are categorized in the general-flowering type, and no large difference in flowering phenology was found among fruit types, except for more frequent reproduction of animal-dispersed species during non-GFP than the others. The predator satiation hypothesis assumes generalist fruit predators, mainly birds and mammals, as predators to be saturated. However, generalist vertebrate predators are unlikely to eat small seeds like those of orchids, and yet these species also flowered more heavily 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 generalist predators has yet to be supported by field data.

Predator satiation at the level of a species or a group of related species sharing common fruit predators may also be important. 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, Nagamitsu, and Inoue, 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*. However, specialist seed predator satiation cannot explain flowering synchronization among various species, because species of seed predators to be saturated are different among plant groups.

Considering that pollinators and predators have also been adapted to the general-flowering phenomenon, it is not simple to identify the most important factor for general flowering. Detailed observations of plant-pollinator interactions, response of flower visitors to general flowering, and examination of flowering triggers may be needed to explore the driving force and the scenario for the evolution of general flowering. Further, examination of the relationship between plant characteristics and reproductive phenology as conducted in this study and accumulation of more data on reproductive phenology in the forests are needed.

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APPENDIX. A list of species with numbers of individual plants observed from a canopy observation system (TW) and observed from the forest floor (FF) with life-form types (LFM), pollination system (PS) determined by (Det) observations or collections of flower visitors or floral characters, fruit type (FR), and flowering type (FT).

Family	Species	LFM <sup>a</sup>	Census		Pollination		FR <sup>d</sup>	FT <sup>e</sup>	
			FF	TW	PS <sup>b</sup>	Det <sup>c</sup>			
Anacardiaceae	<i>Bouea</i> sp.	3		1	BT	e	a	G	
	<i>Camposperma auriculatum</i>	G		4	BT	e	l	NF	
	<i>Gluta macrocarpa</i>	3		1	BT	e	l	NF	
	<i>G. wallichii</i>	4	1	1	BT	e	l	G	
	<i>Mangifera havilandii</i>	3		1	BT	e	a	NG	
	<i>M. magnifica</i>	4	2	2	BT	e	a	G	
	<i>Melanochyla</i> aff. <i>beccariana</i>	3		1	BT	e	l	NF	
	<i>Parishia sericea</i>	4		2	BT	e	l	NF	
	<i>P.</i> sp.	4		1	BT	e	l	NF	
	<i>Swintonia shwenkii</i>	4		2	BT	e	l	NF	
	Genus unknown sp.	3		1	BT	e	l	NF	
	Annonaceae	<i>Artabotrys venustus</i>	L		2	C	c	l	A
		<i>Cyathostemma</i> sp.	L		1	C	c	l	NF
		<i>Desmos</i> cf. <i>chinensis</i>	L		1	C	c	l	S
<i>Enicosanthum macranthum</i>		3	1		C	c	l		
<i>Fissistigma kingii</i>		L		1	C	e	l		
<i>F. latifolium</i>		L		2	C	c	l	NF	
<i>Mezzettia havilandii</i>		4	1	1	C	e	a		
<i>Monocarpia euneura</i>		3		2	C	c	l	A	
<i>Polyalthia hypoleuca</i>		3		1	C	e	a		
<i>P. rumphii</i>		2		1	C	c	a	NG	
<i>Pyramidanthe prismatica</i>		L		4	C	c	l	G	
<i>Uvaria desmoides</i>		L		1	C	c	l	A	
Apocynaceae		<i>Anodendron candolleianum</i>	L		1	BO	e	s	NG
		<i>Urceola</i> sp.	L		1	BT	c	a	NF
	Genus unknown sp.	L		1					
Aquifoliaceae	<i>Ilex</i> sp.	4	1	1	BT	e	a	NG	
Araceae	<i>Pothos</i> sp.	E		1				NF	
	<i>Scindapsus coriaceus</i>	E		1				NF	
Araliaceae	<i>Arthropphyllum diversifolium</i>	4		1	BT	e	l	NF	
Schefflera sp.	<i>Schefflera</i> sp.	E		1	BT	e	a		
	<i>Gongronema</i> sp.	L		2	BT	c	s	A	
Hoya sp.	<i>Hoya</i> sp.	E		1	BT	e	s	G	
	<i>Coelostegia griffithii</i>	4	2	1	C	c	l	NG	
Bombacaceae	<i>Durio</i> sp.1	2		1			a	NF	
	<i>D.</i> sp.2	3	1				a		
	<i>D.</i> sp.3	3	1				a		
Burseraceae	<i>Canarium caudatum</i>	4	1	2	BT	c	a	NG	
	<i>C. denticulatum</i>	3		1	DI	c	a	G	
	<i>C. pilosum</i>	3		1	BT	e	a	NF	
	<i>C.</i> sp. C by Kochummen	3		2	BT	e	a	NF	
	<i>C.</i> sp.	4		1			a	NF	
	<i>Dacryodes incurvata</i>	4	1	1	BT	c	a	G	
	<i>D.</i> sp.	3		1	BT	e	a	NF	
	<i>Santiria griffithii</i>	4		1	BT	c	l	G	
	<i>S. laevigata</i>	4	1	1	BT	c	l	NG	
	<i>S. mollis</i>	3	1	4	BT	e	l	A	
	<i>S.</i> sp. G by Kochummen	3		1	BT	e	l	G	
	<i>S. tomentosa</i>	4	1		BT	e	l		
	<i>Scutinanthe brunnea</i>	5	2		BT	e	a		
	<i>Triomma malaccensis</i>	5	1	1	DI	c	s	G	
	Genus unknown sp.1	3		1	BT	e		NF	
	sp.2	4	1	2	BT	e		G	
	Celastraceae	<i>Lophopetalum glabrum</i>	3		3	BT	c	s	G
<i>L. multinervium</i>		4		1			s	G	
Chrysobalanaceae	<i>Atuna excelsa</i>	3		1	BA	e	l	NF	
	<i>Parastemon urophyllum</i>	4	1	2	BA	o	l	G	
Compositae	<i>Vernonia arborea</i>	3		1	BA	e	s	G	
Connaraceae	<i>Agelaea borneensis</i>	L		1	BT	e	a	G	
	<i>A. macrophylla</i>	L		1	BT	e	a	NF	
	<i>Connarus euphlebius</i>	2		1	BT	e	a	G	

## APPENDIX. Continued.

Family	Species	LFM <sup>a</sup>	Census		Pollination		FR <sup>d</sup>	FT <sup>e</sup>	
			FF	TW	PS <sup>b</sup>	Det <sup>c</sup>			
Convolvulaceae	<i>Erycibe</i> sp.	L		1	BT	c	a	NG	
Crypteroniaceae	<i>Crypteronia griffithii</i>	3		2	BT	c	s	NG	
Dilleniaceae	<i>Tetracera macrophylla</i>	L		1	BA	e	a	NF	
Dipterocarpaceae	<i>Cotylelobium melanoxylon</i>	5	1	1			1	NG	
	<i>Dipterocarpus acutangulus</i>	5	1	3	C	e	1	G	
	<i>D. geniculatus</i>	5	3	6	C	c	1	G	
	<i>D. globosus</i>	5		4	BA	c	1	G	
	<i>D. pachyphyllus</i>	5	10	13	L	c	1	G	
	<i>D. palembanicus</i>	4	1	6	C	c	1	G	
	<i>D. tempehes</i>	5	1	1	BA	c	1	G	
	<i>Dryobalanops aromatica</i>	5	9	11	BA	c	1	G	
	<i>D. lanceolata</i>	5	10	5	BA	c	1	G	
	<i>Hopea griffithii</i>	3		3	C	e	1	NG	
	<i>Parashorea lucida</i>	5		1	BA	o	1	NG	
	Shorea sect. <i>Anthoshorea</i>								
		<i>S. confusa</i>	5	1	1	C	c	1	G
		<i>S. ochracea</i>	5	1	1	C	c	1	G
	sect. <i>Brachypterae</i>								
		<i>S. bullata</i>	5	4	6	C	c	1	G
		<i>S. fallax</i>	5	1	2	C	e	1	G
		<i>S. kunstleri</i>	5	4		C	c	1	
		<i>S. scaberrima</i>	5		1	C	e	1	NF
		<i>S. smithiana</i>	5	9	11	C	c	1	G
	sect. <i>Multica</i>								
		<i>S. acuta</i>	5		1	C	e	1	NF
		<i>S. curtisii</i>	5	2	3	C	e	1	G
		<i>S. ferruginea</i>	5	4	5	C	c	1	G
		<i>S. leprosula</i>	5	1	2	C	e	1	G
		<i>S. macroptera</i> ssp. <i>baillonii</i>	5	1	3	C	e	1	NF
		<i>S. macroptera</i> ssp. <i>macropterifolia</i>	5	1	3	C	c	1	G
		<i>S. parvifolia</i>	5	8	9	C	c	1	G
		<i>S. quadrinervis</i>	5	1	2	C	e	1	NF
		<i>S. slootenii</i>	5	1	1	C	e	1	NF
	sect. <i>Pachycarpae</i>								
		<i>S. beccariana</i>	5	7	5	C	c	1	A
		<i>S. macrophylla</i>	5	1	2	C	c	1	NF
	<i>S. pilosa</i>	5	6	6	C	c	1	G	
sect. <i>Richetioides</i>									
	<i>S. faguetiana</i>	4	2	2	C	e	1	G	
	<i>S. xanthophylla</i>	5	1	1	C	c	1	G	
sect. <i>Rubella</i>									
	<i>S. rubella</i>	5		2	C	e	1	NG	
sect. <i>Shorea</i>									
	<i>S. biawak</i>	4		4	C	e	1	NF	
	<i>S. exelliptica</i>	5	3	3	C	e	1	G	
	<i>S. falciferoides</i>	5	1	3	C	c	1	G	
	<i>S. havilandii</i>	5	1	2	C	c	1	G	
	<i>S. obscura</i>	5		1	C	e	1	G	
	<i>S. superba</i>	5	3	4	C	c	1	G	
	<i>Vatica badiifolia</i>	4		1	C	e	1	G	
	<i>V. micrantha</i>	4		2	C	c	1	NG	
	<i>V. aff. parvifolia</i>	4		3	C	e	1	NG	
Ebenaceae	<i>Diospyros pendula</i>	3		1	C	e	1	NG	
	<i>D. sumatrana</i>	2		1	C	e	1	NF	
Elaeocarpaceae	<i>Elaeocarpus nitidus</i>	3		1	BT	c	a	A	
	<i>Sloanea javanica</i>	3		1	BT	e	s	NF	
Euphorbiaceae	<i>Blumeodendron kurzii</i>	4		2	BT	e	1	NG	
	<i>Cephalomappa beccariana</i>	4		1	DI	c	1	G	
	<i>Cleistanthus brideliifolius</i>	3		1	BT	e	1	NF	
	<i>C. pseudopodocarpus</i>	3		1	BA	c	1	G	
	<i>C. sumatranus</i>	3		1	BT	c	1	G	
	<i>C. venosus</i>	3		3	BA	e	1	G	

## APPENDIX. Continued.

Family	Species	LFM <sup>a</sup>	Census		Pollination		FR <sup>d</sup>	FT <sup>e</sup>	
			FF	TW	PS <sup>b</sup>	Det <sup>c</sup>			
Euphorbiaceae	<i>Drypetes iliae</i>	4		1	DI	e	l	G	
	<i>D. longifolia</i>	2	5		DI	c	a		
	<i>D. sp.1</i>	3		1	DI	e	l	S	
	<i>D. sp.2</i>	2		1	DI	e	l	NF	
	<i>Endospermum diadenum</i>	G		1	BT	e	l	S	
	<i>Glochidion sp.</i>	2		1	BT	e	a	NF	
	<i>Koilodepas laevigatum</i>	3		5	BT	c	l	G	
	<i>Macaranga confiera</i>	G		1	BT	e	a	NF	
	<i>M. gigantea</i>	G		1	BT	e	a	NF	
	<i>M. hosei</i>	G		13	BT	e	a	A	
	<i>M. trachyphylla</i>	G		3	BT	e	a	G	
	<i>M. sp.</i>	2		1	BT	e	a	G	
	<i>Mallotus leucodermis</i>	4	2	5	BT	e	l	G	
	<i>M. penangensis</i>	3		2	BT	c	l	G	
	<i>Omphalea bracteolata</i>	L		2	BT	e	l	S	
	<i>Pimelodendron griffithianum</i>	3		1	BT	e	a	G	
	<i>Tapoides villamilii</i>	3		3	DI	c	l	G	
	<i>Trigonopleura malayana</i>	3		1	BA	c	a	G	
	Fagaceae	<i>Lithocarpus ferrugineus</i>	4		1	DI	c	l	A
		<i>L. leptogyne</i>	3		1	DI	e	l	
<i>L. meijeri</i>		4	1		DI	e	l		
<i>Quercus merrillii</i>		3		1	DI	e	l		
Flacourtiaceae	<i>Hydnocarpus anomala</i>	4	1		DI	e	l		
	<i>Guttiferae</i>								
Guttiferae	<i>Calophyllum hosei</i>	4		1	BA	e	l	G	
	<i>C. igneum</i>	4	1		BA	e	l		
	<i>C. nodosum</i>	4		2	BA	e	l	NG	
	<i>C. sp.</i>	2		1	BA	e	l	NF	
	<i>Garcinia parvifolia</i>	3		1	BT	e	a		
	<i>G. sp.</i>	4	1	1	BT	e	a	NG	
	<i>Mesua macrantha</i>	4		1	BA	e	l	NG	
	Icacinaceae	Genus unknown sp.	L		4	C	c	a	G
		Ixonanthaceae	<i>Allantospermum borneensis</i>	4		9	BA	c	l
	Lauraceae		<i>Alseodaphne insignis</i>	4	1	2	BT	e	a
<i>Beilschmiedia phoebeopsis</i>		4		1	BT	e	a	NG	
<i>B. turfosa</i>		4	1		BT	e	a		
<i>Cinnamomum javanicum</i>		3		1	BT	e	a	NG	
<i>Endiandra clavigera</i>		3		1	DI	c	a	S	
<i>Eusideroxylon zwageri</i>		4	4				a		
<i>Litsea petiolata</i>		4	1	1	BT	e	a	A	
<i>Phoebe sterculioides</i>		4	1		BT	e	a		
Genus unknown sp.		4		1			a	NG	
Lecythidaceae		<i>Barringtonia curranii</i>	3	1	1	L	e	l	G
		Leguminosae	<i>Archidendron microcarpum</i>	3		1	BA	c	a
<i>Callerya nieuwenhuisii</i>			L		2	BO	c	l	NG
<i>C. vasta</i>	4		4	3	BO	c	l	G	
<i>Crudia sp.</i>	4			1	BA	e	l	NF	
<i>Dialium indicum</i>	4		1	1	BA	e	a		
<i>D. kustleri</i>	4			1	BA	e	a	NF	
<i>D. platysepalum</i>	4		1	1	BA	e	a	NG	
<i>D. turbinatum</i>	4			1	BA	e	a	NF	
<i>Koompasia excelsa</i>	5		1	3	BA	e	s	G	
<i>K. malaccensis</i>	5		3	3	BA	e	s	G	
<i>Parkia singularis</i>	3			1	M	o	l	NG	
<i>P. speciosa</i>	3			1	M	o	l	G	
<i>Sindora beccariana</i>	5		1	1	BT	c	l	NG	
<i>S. ferrugineus</i>	L			2	BA	c	s	NG	
<i>S. irpicina</i>	5		1		BT	c	l		
<i>S. macropterus</i>	L			1	BA	c	s	NF	
<i>S. multiflorus</i>	L		1	DI	c	s	G		
<i>S. velutina</i>	5	1	1	BT	c	l	NF		
<i>Spatholobus auricomus</i>	L		1				NF		
<i>S. sp.1</i>	L		1	BA	e	s	G		
<i>S. sp.2</i>	L		1	BA	e	s	NG		
Genus unknown sp. 1	L		1				NF		
sp.2	L		1				NF		
sp.3	L		1				NF		
sp.4	L		1				NF		

## APPENDIX. Continued.

Family	Species	LFM <sup>a</sup>	Census		Pollination		FR <sup>d</sup>	FT <sup>e</sup>	
			FF	TW	PS <sup>b</sup>	Det <sup>c</sup>			
Linaceae	<i>Indorouchera griffithiana</i>	L		1				NF	
Loganiaceae	<i>Strychnos polytrichantha</i>	L		1			l	NF	
Loranthaceae	<i>Amylothea duthieana</i>	E		3	A	c	a	A	
	<i>Trithecanthera xiphostachys</i>	E		1	A	c	a	A	
	Genus unknown sp.	E		1	A	e	a	S	
Magnoliaceae	<i>Magnolia gigantifolia</i>	2		1	C	e	a	NF	
Melastomataceae	<i>Diplectria stipularis</i>	L		1	BT	e			
	<i>Memecylon</i> sp.	3		1	BT	e	a	NF	
	Genus unknown sp.	L		1				A	
Meliaceae	<i>Aglaia korthalsii</i>	4	1		BT	e	a		
	<i>Chisocheton sarawakensis</i>	3		1	BO	e	a	G	
Menispermaceae	<i>Coscinium wallichianum</i>	L		1					
Moraceae	<i>Artocarpus aniosophyllus</i>	4	2	2	DI	e	a	NF	
	<i>A. dadah</i>	4		1	DI	e	a	NF	
	<i>A. elasticus</i>	4	2	1	DI	c	a	G	
	<i>A. integer</i>	4	3	1	DI	c	a	NF	
	<i>A. melinoxylus</i>	4	1		DI	e	a		
	<i>A. nitidus</i>	4		1	DI	e	a	A	
	<i>A. odoratissimus</i>	4	1	2	DI	c	a	G	
	<i>A. tamaran</i>	4	1		DI	e	a		
	<i>Ficus benjamina</i>		1		F	e	a		
	<i>F. binnendykii</i>			1	F	e	a	A	
	<i>F. consociata</i>			1	F	e	a	S	
	<i>F. deltoidea</i>			1	F	e	a	S	
	<i>F. kerkhovenii</i>		2	3	F	e	a	S	
	<i>F. microcarpa</i>			1	F	e	a		
	<i>F. pellucidopunctata</i>			1	F	e	a	A	
	<i>F. subcordata</i>			1	F	e	a	A	
	<i>F. sumatrana</i>			1	F	e	a	A	
	<i>F. xylophylla</i>			2	F	e	a	NG	
	Myristicaceae	<i>Prainea frutescens</i>	3		1	DI	e	l	NF
		<i>Gymnacranthera contracta</i>	4		2	C	c	a	A
<i>Horsfieldia grandis</i>		3		1	O	c	a	G	
<i>H. pallidicaula</i>		3		1	O	e	a		
<i>H. polyspherula</i>		3		1	O	e	a		
<i>Knema cinerea</i>		4	1		C	c	a		
<i>K. furfuracea</i>		3		1	C	e	a	NF	
<i>K. laterica</i>		3		2	C	e	a	G	
<i>K. latifolia</i>		3		3	C	c	a	A	
<i>K. pedicellata</i>		3		1	C	e	a	G	
<i>K. sp.1</i>		3		1	C	e	a	A	
<i>K. sp.2</i>		3		1	C	e	a	NG	
<i>K. sp.3</i>		2		1	C	e	a	NF	
<i>Myristica malaccensis</i>		3		1	C	e	a	NF	
<i>M. villosa</i>		4		2	C	e	a	A	
<i>M. sp.</i>		4	1	1	C	e	a	A	
Myrsinaceae		<i>Ardisia macrophylla</i>	3		1	A	o	a	G
Myrtaceae	<i>Eugenia ochneocarpa</i>	3		1	DI	e		A	
	<i>E. roslenta</i>	4		1	DI	e		NF	
	<i>E. subrufa</i>	4	2	2	DI	c		G	
	<i>E. sp.1</i>	4		1	DI	e		NF	
	<i>E. sp.2</i>	3		1	DI	e		G	
	<i>E. sp.3</i>	4	1		DI	e			
	<i>E. sp.4</i>	4	1	2	DI	c	l	NG	
	<i>E. sp.5</i>	3		1	DI	e		NF	
	Genus unknown sp.	4		1	DI	e		G	
	<i>Ochanostachys amentacea</i>	3		1	BT	e	a	G	
Olacaceae	<i>Scorodocarpus borneensis</i>	4		1	BT	c	l	NG	
	<i>Trias</i> sp.	E		1	BA	c	s	G	
Orchidaceae	Genus unknown sp.1	E		1			s	NF	
	sp.2	E		1			s		
	sp.3	E		1			s	NF	
	sp.4	E		1			s	NF	
	sp.5	E		1			s	NF	
	sp.6	E		1			s	A	
	sp.7	E		1			s	G	
	sp.8	E		1			s	G	

## APPENDIX. Continued.

Family	Species	LFM <sup>a</sup>	Census		Pollination		FR <sup>d</sup>	FT <sup>e</sup>
			FF	TW	PS <sup>b</sup>	Det <sup>c</sup>		
Orchidaceae	Genus unknown sp.9	E		1			s	G
	sp.10	E		1			s	NG
	sp.11	E		1			s	
Pandanaceae	<i>Freycinetia winkleri</i>	E		2			a	NG
Piperaceae	<i>Piper</i> sp.	L		1	DI	e	l	A
Rhizophoraceae	<i>Carallia brachiata</i>	3		1	DI	c	a	S
Rubiaceae	<i>Porterandia anisophylla</i>	2		1	BO	e	l	NG
	<i>Randia</i> sp.	L		1			l	A
	<i>Uncaria longifolia</i>	L		2	DI	c	s	A
	<i>U.</i> sp.1	L		1			s	A
	<i>U.</i> sp.2	L		1			s	A
Sapindaceae	<i>Nephelium cuspidatum</i>	3	1		BT	c	a	
	<i>Pometia pinnata</i>	4	2	3	BT	c	a	G
	<i>Xerospermum laevigatum</i>	3		1	BT	e	a	G
Sapotaceae	<i>Ganua beccariana</i>	3		3	M	o	a	NF
	<i>G. hirtiflora</i>	4	1				a	
	<i>G.</i> sp.	4	1		M	e	a	
	<i>Palaquium calophyllum</i>	4	1		BT	e	a	
	<i>P.</i> sp.	4	1	1			a	G
	Genus unknown sp.	5	1				a	
Simaroubaceae	<i>Irvingia malayana</i>	4	1				l	
	<i>Quassia borneensis</i>	4	2	2	DI	c	l	A
Sterculiaceae	<i>Heritiera borneensis</i>	5	1	2	C	c	l	NG
	<i>H. impressinervia</i>	4	1		C	e	l	
	<i>H. sumatrana</i>	5	3	4	C	c	l	G
	<i>H.</i> sp.	5		1	C	e	l	
	<i>Pterocymbium tubulatum</i>	5	1		BA	c	l	
	<i>Pterospermum fuscum</i>	G	1		M	e	s	
	<i>Scaphium borneense</i>	4		3	BA	c	l	G
Theaceae	<i>S. longipetiolatum</i>	5	2	2	BT	c	l	G
	<i>Sterculia</i> sp.	4	1		C	e	l	
	<i>Eurya acuminata</i>	2		1	BT	c	a	A
	<i>Amyxa pluricornis</i>	3		1	DI	e	a	G
Thymelaeaceae	<i>Gonystylus forbesii</i>	3		1	DI	e	a	G
	<i>G. micranthus</i>	3		1	DI	e	a	
	<i>Linostoma pauciflorum</i>	L		1	DI	e	a	NG
Tiliaceae	<i>Pentace adenophora</i>	3		1	BT	e	s	NF
	<i>Schoutenia glomerata</i>	3		2	DI	c	s	NF
Ulmaceae	<i>Gironniera nervosa</i>	4		1				NG
Verbenaceae	<i>Callicarpa pentandra</i>	G		1	BT	c	a	S
	<i>Sphenodesme triflora</i>	L		4	BO	e	s	NG
	<i>Teijsmanniodendron simplicifolium</i>	3		2	DI	c	a	NG
Xanthophyllaceae	<i>Xanthophyllum</i> sp.	3		1	BO	e	a	NG
Zingiberaceae	Genus unknown sp.	E		1				NF
Family, genus unknown	sp.1	E		1				G
	sp.2	E		1				A
	sp.3	L		1				NF
	sp.4	E		1				NG
	sp.5	L		1				NG
	sp.6	E		1				NG
	sp.7	E		1				NF
	sp.8	L		1				NG
	sp.9	L		1				NF
	sp.10	L		1				A
	sp.11	G		1				S
Total			194	486				

<sup>a</sup> 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. *Ficus* spp. are excluded from this classification.

<sup>b</sup> See Table 2.

<sup>c</sup> e, estimated by floral characters; c, determined by collection of flower visitors; o, determined by observation of flower visitors.

<sup>d</sup> a, animal dispersed; l, large fruit; s, small fruit.

<sup>e</sup> S, sub-annual; A, annual; G, general flowering; NG, supra-annual; NF, nonflowering.