4. Plant Reproductive Phenology and General Flowering in a Mixed Dipterocarp Forest

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This chapter discusses the flowering patterns at Lambir Hills observed by the Canopy Biology Program in Sarawak (CBPS), in the current perspective of tropical phenology. We begin with a review of phenological studies, mostly from seasonal forests having dry seasons, in the Neotropics. Next, the flowering phenology of lowland dipterocarp forests, characterized by general flowering (GF), is described, comparing and contrasting the flowering tempo of this forest to that found in other forests. Then, the ultimate and proximate causes of flowering phenology are reviewed. A discussion of future directions and challenges concludes the chapter.

4.1 Introduction

Phenology is the study of the periodicity or timing of recurring biological events, in relation to short-term climatic change. In the case of plants, phenological events involve flowering, fruiting, leaf flushing, and seed germination (Leith 1974). The timing of these events can profoundly affect survival and reproductive success. Not only abiotic environmental factors such as temperature and humidity, but also biotic elements including herbivory, competition, and pollination (through pollinators and flowering phenology of other conspecifics) can be selective agents for patterns of plant phenology. Germination, flowering, or leaf production at the wrong time cause low survivorship of seedlings (Tevis

1958), low seed production (Augspurger 1981), and high predation rates (Aide 1992), respectively. At the same time, plant phenology can greatly affect animals that use young leaves, flowers, seeds and mature or immature fruits (van Schaik et al. 1993), and resource cycling in the forest. Plant phenology is thus of fundamental importance for monitoring, managing, and conserving ecosystems. Most studies of plant phenology in tropical forests have been conducted to describe resource availability for consumer animals (e.g., Frankie et al. 1974; Croat 1975; Putz 1979; Opler et al. 1980; Foster 1982; Koptur et al. 1988; Murali and Sukumar 1994; Justiniano and Frederickens 2000; Morellato et al. 2000). Other studies emphasize physiological release mechanisms (e.g., Augspurger 1981; Reich and Borchert 1982) and synchronization within populations (e.g., Augspurger 1980, 1983; Primack 1980) from a perspective of plant reproductive success by monitoring the focal plants in more detail at the population level for rather short time periods. Further aspects of plant phenological studies are reviewed in Rathcke and Lacey (1985), Primack (1987) and van Schaik et al. (1993).

One central characteristic of phenology in tropical forests may be high diversity, which has two important aspects (Gentry 1974; Janzen 1978; Bawa 1983; Sarmiento and Monasterio 1983; Newstrom et al. 1994a, b). First, phenology patterns may be quite different among individuals of a given species, thus the flowering or fruiting pattern of individual plants may differ from the mean of the population and community. For example, flowering of *Boesenbergia grandifolia* (Zingiberaceae) in Borneo has irregular sub-annual or annual flowering patterns at the individual level but continuous flowering at the population level (Sakai 2000). Second, various flowering patterns are found among plants in the local community. Gentry (1974) was among the first to draw attention to the high diversity in phenology in tropical forests, compared to forests in the Temperate Zone. He qualitatively classified flowering phenology of the Bignoniaceae in four flowering types based on duration, frequency, and amplitude and discussed the ecological significance of such differences in relation to pollination. His work demonstrated the great potential of tropical phenological studies for exploring selective pressures and their evolutionary significance.

4.2 Annual Cycles at the Community Level in Seasonal Forests

Climate in tropical rain forests is characterized by continuous humid or warm conditions, which potentially allow most organisms to remain active throughout the year. Thus, one prominent theme in tropical community studies is the degree of periodicity or regularity of biological activities. In the temperate region, regular rhythms in temperature, day length, and winter, which limits all biological activities, impose clear annual cycles. In contrast, in the low latitudes the difference between the shortest and the longest day of the year is small: about 70 minutes at 10° latitude. The annual range of mean temperature is much smaller than changes during a day. The nights are the winter of the tropics. However, a periodic change in rainfall caused by movements of the intertropical convergence zone, a seasonal event in the tropics, rather than temperature and day length, plays an important part in controlling proximate and ultimate factors for tropical plant phenology (van Schaik et al. 1993). Dry seasons within an annual cycle occur in most tropical regions, and many studies have shown a correlation between phenology and rainfall (Augspurger 1981; Borchert 1983; Reich and Borchert 1984). Most Neotropical forest communities that have been studied show flowering and fruiting peaks near the end of the dry season (Janzen 1967; Croat 1975; Foster 1982; Frankie et al. 1974; Hilty 1980; Opler et al. 1980; Bullock and Solis-Magallanes 1990; Justiniano and Fredericksen 2000). The pattern may be due to high insolation and photosynthesis in dry seasons. Alternatively, or in addition, it may enhance germination and seedling survival by adjusting fruiting to precede the beginning of the wet season (van Schaik et al. 1993).

Although the effect of rainfall pattern are predominant even in wet forests without a clear dry season, detailed examination at the species and population levels can reveal wide variation in flowering phenology. At La Selva, in Costa Rica, most trees have a sub-annual flowering pattern (55% of 254 species flower more than once a year, often irregularly), and only 29% of trees show an annual flowering pattern (see Fig. 4.1; Newstrom et al. 1994b). This forest is wet and lacks a severe dry season; monthly precipitation never drops lower than 100 mm (Sanford et al. 1994).

While comparative data are not available from other Neotropical forests, a higher proportion of annual flowering species may occur in forests with stronger seasonality. Wright and Calderon (1995) analyzed flowering phenology of 217 species with 230 seed traps for five years on Barro Colorado Island (BCI) in Panama. They found that flowering was highly concentrated in time for most species, and mean flowering dates of species were concentrated in February and March, which are the driest months of the year, and in April and May when the wet season begins. In addition, year-to-year variation in intensity of plant reproduction may also be related with rainfall fluctuation. As one example, in the moist forest of BCI, an infrequent famine was shown to be linked to an unusually small fruit crop during a La Niña year (moderate dry season) that followed an El Niño-Southern Oscillation event (Wright et al. 1999).

Although many studies have reported the clear correlation between rainfall patterns and phenological events, results of irrigation experiments are not always positive. Some biologists have succeeded in manipulating flowering phenology by watering plants (Augspurger 1981; Reich and Borchert 1982; Wright and Cornejo 1990a, b; Wright 1991; Tissue and Wright 1995). However, a large-scale irrigation experiment (2.25 ha) in BCI, with a strong seasonal pattern in rainfall, showed that irrigation had no effect on the timing of leaf fall, leaf flush, flowering, or fruiting for most species of canopy trees (Wright and Cornejo 1990a,b). Deep-rooting canopy trees possibly do not experience a water deficit even in dry seasons (Steinberg et al. 1989). The mechanisms for synchronized flowering are still unknown, and little is known about consequences.

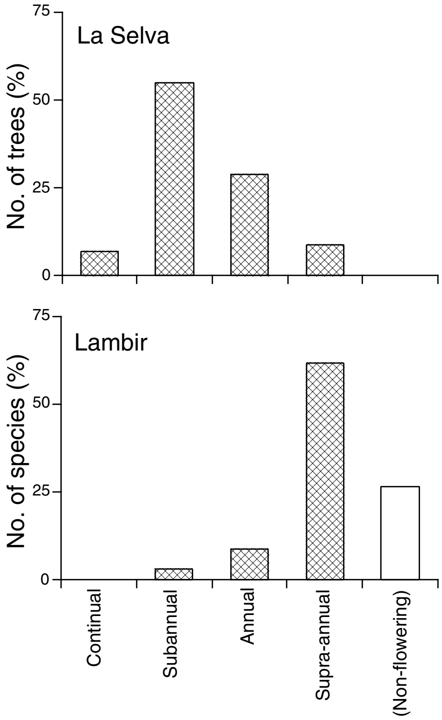

Figure 4.1. Proportions of sub-annual, annual, supra-annual and continual flowering types among trees at La Selva, Costa Rica (254 species, Newstrom et al. 1994b) and Lambir, Malaysia (187 species, Sakai et al. 1999c); modified from Sakai 2002. The General Flowering at Lambir is included in supra-annual. Note La Selva is on an individual tree basis, Lambir on a species basis; Newstrom et al. (1994b) state the two are similar at La Selva.

4.3 Flowering Phenology in Southeast Asia

In a large portion of the Asian tropical forests from Sumatra to the Philippines, there is generally no clear annual cycle of rainfall (Yasunari 1995; McGregor and Nieuwolt 1998). It is here that flowering at multi-year intervals—called GF, general flowering or mass-flowering—is known from lowland dipterocarp forests (Ashton et al. 1988). A GF usually occurs every 2 to 10 years. During GF, many trees, including most dipterocarps and other families, flower for months, yet some flowering occurs in non-GF periods (Sakai et al. 1999c; Sakai 2002). The longest records of GF comes from statistics of exports, since GF brings about a huge crop of *illipe nuts* (fruits of *Shorea* section *Pachycarpae*), an important commercial item of the region for export (Blicher 1994) and thus has a strong effect on the local economy.

Although the importance and uniqueness of the GF have been stressed by other authors (Janzen 1974; Appanah 1985, 1993; Ashton 1989; Ashton et al. 1988), there are few detailed studies that accurately describe a GF at the community level, or that examine the prevalence of the phenomenon among species of different life forms, the pollination mode, or the fruit dispersal. Records of gregarious flowering in most studies are restricted to the Dipterocarpaceae (Burgress 1972; Ng 1977; Yap and Chan 1990) or inferred by examination of herbarium specimens (Cockburn 1975). A few studies on GF 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 GF to non-GF cycle (Corlett 1990).

One of the major purposes of CBPS concerned the causes and consequences of GF (Chapter 2). To accomplish this study, in 1992 the CBPS began monitoring phenological events among 576 plants of 305 species. Observations were comprehensive within the study site, using tree towers and aerial walkways constructed in an 8 ha permanent plot (Sakai et al. 1999c; Inoue et al. 1995; Yumoto et al. 1996). When the censuses were initiated, the forest was at a fruiting peak following the GF of 1992. From 1993 to 1995, the proportion of flowering plants was very low, around 3%. However, in May 1996, the proportion increased dramatically to reach 17% and 20% for individuals and species, respectively. Thus, this GF was observed from its beginning (see Fig. 4.2; Sakai et al. 1999c). To our surprise, the proportion of plants flowering had two peaks in 1996, and GFs were also observed during the following two years.

The percentage of plants in flower was generally quite low in Lambir Hills, compared with other tropical regions (see Table 4.1). In most seasonal lowland forests, the proportions of species flowering average 15% to 20%. In tropical forests at higher elevations, the proportion can be higher. In a forest with a severe dry season the number of flowering species often drops to zero for a few very dry months each year, but at other times it is over 10% and sometimes exceeds 60% (Murali and Sukumar 1994). The maximum proportion recorded at Lambir Hills so far, 22%, is also much lower than the maxima observed in other forests. Medway (1972) reported similar figures to those of Lambir Hills from a lowland dipterocarp forest in Peninsular Malaysia.

Sakai et al. (1999c) analyzed the phenology data up until December 1996 to describe plant reproductive phenology and GF in 1996 at Lambir Hills, and they concluded that the low percentage of flowering individuals was mainly due to low flowering frequency and the concentration of reproductive activities in GF periods, only at multi-year intervals. They classified species into flowering types using the flowering data of individual plants for the 43 months from June 1993 to December 1996. The first is a GF type, which flowers only in the GF period. Three additional categories were based on flowering frequency: *supra-annual* (flowered once or twice in 43 months), *annual* (flowered three or four times), and *sub-annual* (flowered more than four times). When a species included individuals that displayed more than one flowering type, the majority represented the species. Species in which reproduction was not observed during the 43 months were tentatively categorized as *non-flowering* (see Fig. 4.1).

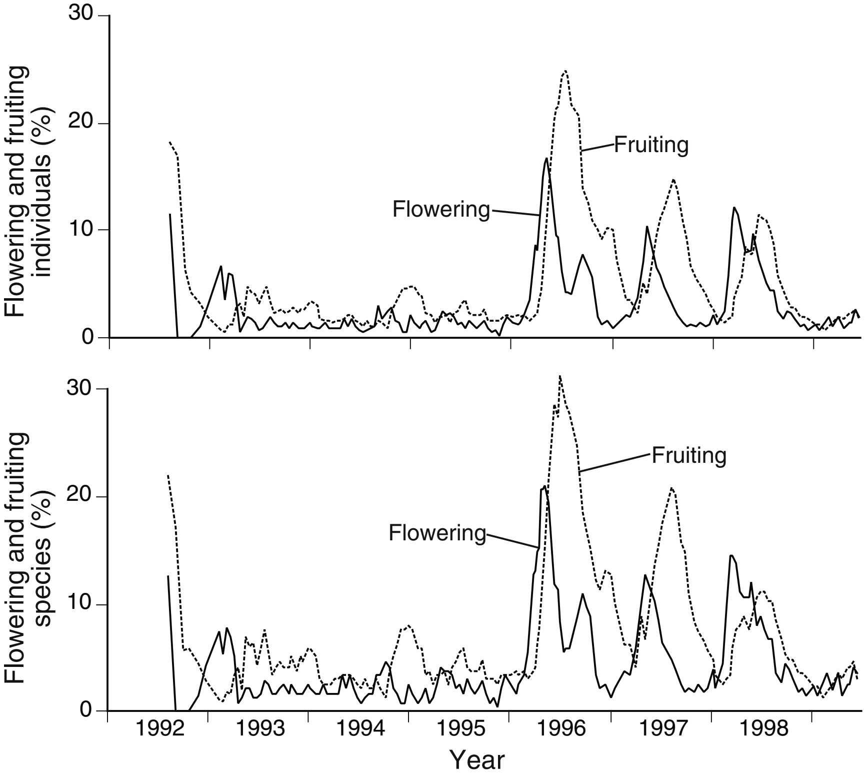

Figure 4.2. Changes in percentage of flowering or fruiting species and individuals observed from tree towers and walkways (237 spp., 428 individuals, Sakai et al. 1999c, Sakai et al., unpublished data).

In contrast to the plants at La Selva, Costa Rica, more than half of the species we observed were supra-annual and GF species, which flower once in two or more years on average. A continuous flowering pattern (extended flowering with short interruptions) was rarely found (see Fig. 4.1). Causes of this difference have scarcely been explored, although a poor nutrient level in the soil was suggested to be a factor (Janzen 1974; Inoue 1997). Out of 527 flowering events observed during 43 months from July 1993 to December 1996, 57% occurred in 10 months of GF from March to December 1996. Among species that flowered at least once in the 43 months, 85% reproduced during the GF period. Most species showed strict synchronization within species, and major flowering periods of species were usually less than one month long. During a GF, the flowering of related species tended to be aggregated in time (see Fig. 4.3).

Participation in GF was observed among various plant groups, which confirmed that GF was a general phenomenon, operating at the community level.

Table 4.1. Proportion of species recorded as flowering in various tropical forests

Study site	Forest type	Flowering spp. %	References
Neotropics			
La Selva (Costa Rica)	Wet, lowland	Overstory trees 9–30 Understory trees 17–38	Frankie et al. (1974)
Comelco (Costa Rica)	Dry, lowland	7–28	Frankie et al. (1974)
Monteverde (Costa Rica)	Montane	20–60	Koptur et al. (1988)
Alto Yunda (Clombia)	Premontane	25–40	Hilty (1980)
Lomerio (Bolivia)	Dry, lowland	8–41	Justiniano and Fredericksen (2000)
São Paulo (SE Brazil)	Wet, lowland	3–33	Morellato et al. (2000)
	Premontane	3–24	Morellato et al. (2000)
Africa			
Nyungwe (Rwanda)	Montane	14–47	Sun et al. (1996)
Asia			
Mudumalai (S India)	Dry, lowland	0–60	Murali and Sukumar (1994)
Dipterocarp forests in Asia			
Lambir (Borneo)	Wet, lowland	Non-GF period 0–3 GF–22	Sakai et al. (1999)
Ulu Gombak (Peninsular Malaysia	Wet, lowland	Non-GF period 0–7[a] GF–35[a]	Medway (1972)

[a] Proportion of individuals

As many as 35% of 257 species at Lambir were of the GF type. These comprised plants of different families and life forms, from epiphytic orchids to emergent dipterocarp trees (see Fig. 4.4). Supra-annual and annual species also reproduced more actively during a GF period than during non-GF years (see Fig. 4.5). Therefore, GF is the preeminent reproductive pattern at Lambir.

4.4 Ultimate Factors

Van Schaik et al. (1993) showed that peaks in irradiance are accompanied by peaks in leaf flushing and flowering. These authors reviewed phenological studies from all the three major tropical regions. Their work strongly suggested a major role of climate as a determinant of phenology. They proposed several explanations, including the *high radiation* hypothesis. Since it is energetically most efficient to transfer *photosynthates* directly into growing organs, rather than store them for later translocation (Chapin et al. 1990), it is advantageous for plants to produce leaves and flowers during the most productive season. The hypothesis assumes that plant production is mostly limited by *insolation* and *irradiation* which usually have a peak in the tropical dry season, mainly because of less cloudiness (van Schaik et al. 1993). This general rule was supported by

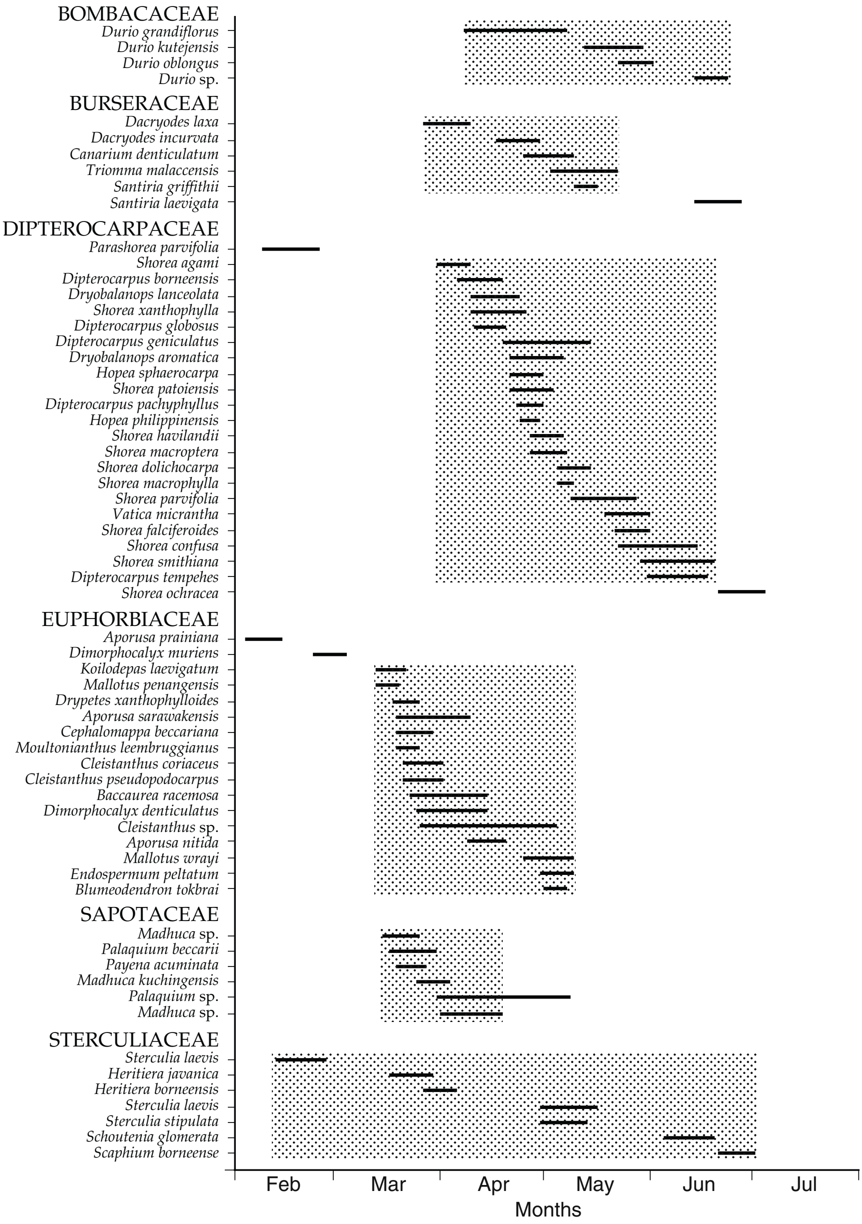

Figure 4.3. Flowering periods of different taxonomic groups at Lambir during 1996 GF (Momose et al. unpublished data).

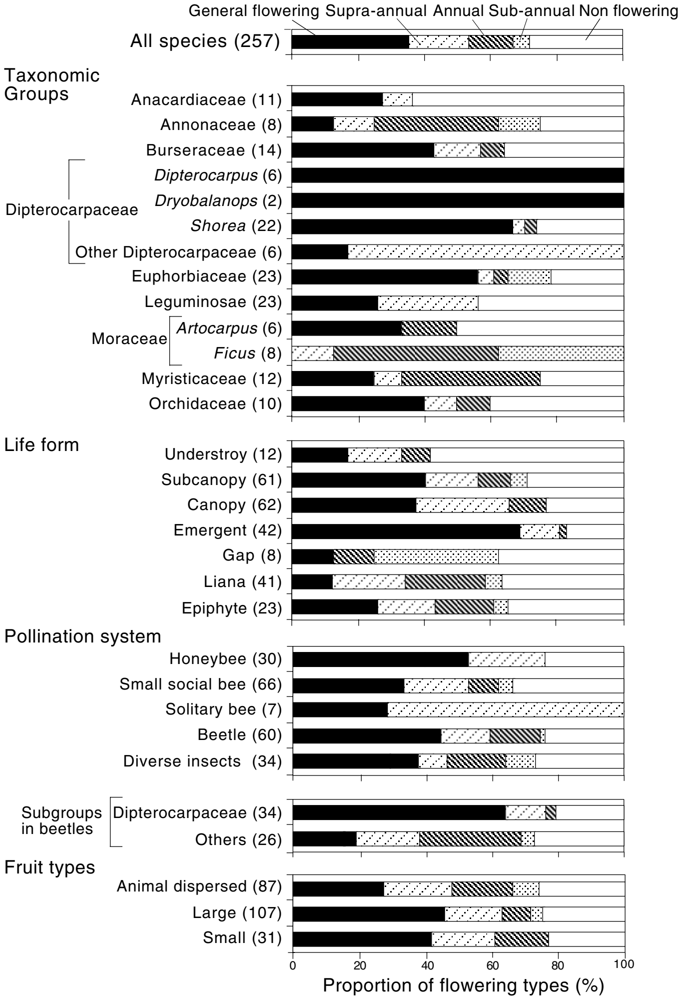

Figure 4.4. Flowering types (sub-annual, annual, and general flowering) and non-flowering species (species not flowering during the observation period) among all species observed, and taxonomic groups, life-form types, pollination systems, and fruit type; N species in parentheses (Sakai et al. 1999c).

the fact that peaks of flowering and flushing occur in the months of most intense and sustained sunshine. Besides, flowering in dry periods and fruit dispersal in the following rainy season may be adaptive, considering water conditions are critical for seed germination and survival in the tropics and that seeds of many tropical plants do not have dormancy. Sakai (2002) suggests that predictable rainy periods of the supra-annual cycle caused by ENSO (El Niño Southern

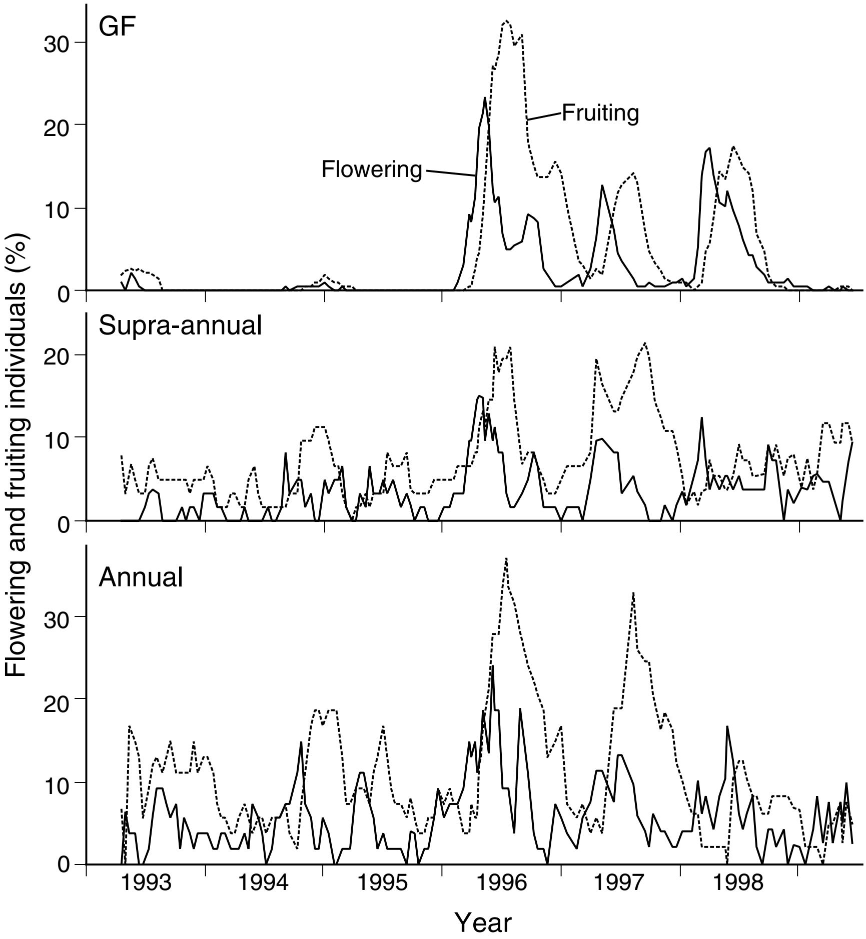

Figure 4.5. Changes in percentage flowering and fruiting individuals for GF, supra-annual and annual flowering types—193, 43, 50 individuals for GF, supra-annual, annual species, respectively (Sakai et al., unpublished data).

Oscillation) may also promote synchronized flowering triggered by drought in Southeast Asia, where rainfall pattern lacks clear annual regularity.

Among biotic factors, predator satiation has been considered to be the most important in explaining supra-annual reproduction in plants. It asserts that synchronized fruiting at long intervals is an effective means of starving the predators in low seed years, or surpassing their needs and satiating them in high years (Janzen 1971b; Silvertown 1980). Although the hypothesis is supported by some field data from temperate forests showing lower per-capita seed predation in mast years (e.g., Sork 1993; Crawley and Long 1995; Kelly and Sullivan 1997), Kelly (1994) accurately pointed out that the validity of the hypothesis depended on the functional response of predators to crop size (Ims 1990). He suggested two possible scenarios: that predator populations or losses of seeds are limited by small crop size during non-mast years, and that predator populations are generally limited by factors other than crop size. If seed predators are specialists, predator populations determined by small crop size in non-masting years are much smaller than would be maintained by constant seed production. The occurrence of consecutive mast years can be evidence against this particular hypothesis. The other case assumes predators are generalists, thus their populations are not limited by crop size of a particular plant species. Plants may only limit predation by producing a crop far beyond the potential amount of predator consumption in a masting year, using resources accumulated in normal years. In the latter case, consecutive masting can function to satiate predators.

Predator satiation has been treated as the most important evolutionary factor for GF (Janzen 1971b). The predators in this case are birds and mammals which consume fruits of a wide range of plants, since satiation of specialized predators such as most insect fruit parasites does not explain synchronized flowering among plants of different genera and families found in GF. The hypothesis is supported by studies from Kalimantan showing the high predation rate of dipterocarp fruits in a minor flowering year, compared to a large one (Curran and Leighton 2000; Curran and Webb 2000). However, Inoue (1997) and Sakai et al. (1999c) indicated that predator satiation does not explain concentration of flowering in GF periods of non-dipterocarp species, including orchids and others with tiny fruits or seeds, which are usually neglected by birds and mammals.

Instead, the above authors suggested that the promotion of pollination, through temporal aggregation of flowering, is a strong evolutionary factor that promoted GF. The idea is contrary to a well-known concept called the "shared pollinator hypothesis," which has received particular attention for tropical forest plants. That hypothesis predicts that plant species sharing common pollinators should separate their flowering somewhat to minimize interspecific overlap in flowering times, and thus minimize ineffective pollination and/or competition for pollinators (Stiles 1977; Ashton et al. 1988). Stiles (1977) documented that Neotropical Costaceae and Heliconiaceae had clear annual rhythms in flowering and suggested strong intraspecific synchronization and temporal segregation among species sharing pollinators. Ashton et al. (1988) showed sequential flowering of *Shorea* species (Dipterocarpaceae), which significantly segregated flowering periods during a few months of GF. However, most experimental or field studies (Wheelwright 1985; Murray et al. 1987; Wright and Calderon 1995) have produced negative results. At Lambir Hills, many ginger species (Zingiberaceae and Costaceae), the most important herbaceous constituents on the forest floor, are pollinated by birds or solitary bees and showed irregular, sub-annual flowering patterns (Sakai et al. 1999a,c; Sakai 2000). Their flowering periods could be both synchronized and unsynchronized among conspecific individuals. Thus no temporal segregation among species sharing common pollinators occurred (Sakai 2000). Other studies suggested that synchronized flowering of different species could facilitate pollination through an increase of resource density and local pollinator attraction (Schemske 1981). Aggregation of flowering in time may be due to pollinator availability in a particular season. In dry deciduous forest, Frankie (1975) found that a disproportionately large number of moth-pollinated plants flower in the wet season. He suggested that this aggregation of flowering time might be related to moth population density, which was controlled by the abundance of new foliage: the larval food (Frankie 1975). Flowering may, however, be completely out of phase with pollinator abundance (Zimmerman et al. 1989).

The "promotion of pollination hypothesis" proposed by Inoue (1997) and Sakai et al. (1999c) assumed a higher pollination success in GF periods than non-GF periods. For this principle to operate, the number of available pollinators relative to flowers must increase rapidly. 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 increase the density of flower visitors through immigration, population growth and feeding. The idea is supported by higher fruit set in GF than in non-GF periods (Yap and Chan 1990; Sakai et al. 1999c). An increase in population density or activities in GF has been observed in some pollinators. Giant honeybees, important pollinators in GF (Momose et al. 1998c), have an ability to migrate long distances, up to 200 km. They are thought to immigrate into dipterocarp forests when GF begins, likely from secondary and montane forests, where some flowers are usually available. Giant honeybees pollinate the two most abundant dipterocarp species (*Dryobalanops lanceolata* and *D. aromatica*) as well as other minor plant species at Lambir Hills (see Chapters 6, 8). Therefore, the minor plants may receive benefits from synchronized flowering with abundant dipterocarps, since flowering of a single rare species cannot induce immigration of giant honey bees. Many pollinators, including many resident bees, become abundant through population growth in GF.

Appanah and Chan (1981) reported that *Shorea* (Dipterocarpaceae) were pollinated by thrips, tiny insects which feed on pollen and floral tissue of a variety of plant species. Because of low specialization to plant species and short generation time, thrips build up large populations quickly at the beginning of GF and serve as pollinators of different *Shorea* spp. On the other hand, Sakai et al. (1999a, b) found that small beetles were the main pollinators of *Shorea* (Dipterocarpaceae) at Lambir Hills. Interestingly, some of the pollinators are herbivores as well, feeding on new leaves of dipterocarp trees and possibly others during non-GF periods without dipterocarp flowers. In this case, a rapid increase of the pollinating beetles is unlikely because they do not migrate or reproduce as rapidly as do thrips. More detailed studies of life history of the pollinator beetles (copulation and breeding sites), and also the host (both for flowers and leaves) are required to clarify relationships between the pollinators and GF.

Momose et al. (1998a) addressed differences in flowering intervals among plants belonging to different forest strata using a theoretical approach. The model assumed that the flowering intervals of trees maximize visits by pollinators, including opportunist and social bees, throughout their lifetimes after they reach mature size. The model also assumed that larger displays attract more opportunist (social) pollinators per flower, while the number of other 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 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 to display heavily and attract many opportunist pollinators. By contrast, the canopy or subcanopy species cannot wait as long between reproductive episodes because of higher mortality. For these trees it is better to frequently produce smaller displays to attract pollinators. 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 giant honeybees (*Apis dorsata*), which respond only to extraordinarily large floral resources associated with GF (Itioka et al. 2001a).

A few studies have focused on differences in flowering patterns among plants with different pollination systems (Gentry 1974; Frankie 1975; Momose et al. 1999a). At Lambir Hills, Sakai et al. (1999c) found a correlation between flowering types and pollination systems, which may be related to characteristics of their pollinators. Because flowers of GF plants are available only during GF, their flower visitors and pollinators should use a wide range of resources in terms of foraging area, resource type, and/or plant species. In contrast, plants with high host-specificity, such as beetle-pollinated Annonaceae and fig-wasp-pollinated *Ficus* tend to flower more frequently (see Fig. 4.4).

Studies from tropical forests and other regions indicate that in addition to ecological factors, flowering phenology is under strong *phylogenetic constraint* (Kochmer and Handel 1986; Johnson 1992; Ollerton and Lack 1992; Wright and Calderon 1995). Plants sharing the same pollinators often show synchronous flowering, simply because they are closely related. The fact is often cited to reject the shared pollinator hypothesis, which depends upon segregated flowering among plants pollinated by the same animals. In the GF period at Lambir Hills, aggregation of flowering periods was found among species of the same taxonomic groups (see Fig. 4.3). Strong phylogenetic constraints detected by the above studies, however, do not necessarily indicate absence of adaptation in phenology. The diversity of tropical flowering phenologies should be guided by such phylogenetic perspectives. This means, for example, that the GF in Southeast Asia has an historical component. We may have to direct more attention to synchronization of flowering among species of different families than primarily within a family or Dipterocarpaceae, or to dipterocarps that do not share GF phenology patterns.

4.5 Proximate Factors

At the mechanistic level, flowering can be thought to be under the control of both internal and external factors. Internal factors include plant developmental stage (immature or mature) and stored resources. External variables are environmental, such as humidity, temperature, or day length. All of these factors are interrelated and function in different ways in different plant species (Bernier 1988). Little is known about which external factors function in observed flowering patterns with high diversity, in the relatively equable climate of the tropical rain forest, except for a few studies on annual-flowering species in the seasonal tropical forests (Reich and Borchert 1982; Augspurger 1981; Rivera and Borchert 2001). Here, we limit our discussion to comment on sub-annual flowering and GF patterns.

Newstrom et al. (1994b) suggested that flowering patterns of irregular, sub-annual flowering could be viewed as due to inhibiting factors, rather than inducing ones, although almost no information exists on mechanisms controlling sub-annual flowering. They reported that some trees of sub-annual species never flowered in a certain month at La Selva, Costa Rica, possibly because certain inhibiting factors occurred annually. Since non-flowering months were different among species, the putative inhibiting factors might also be varied (Newstrom et al. 1994b).

The same may be true for flowering phenology of gingers and *Macaranga* at Lambir Hills. Some ginger species flower intermittently, while flowering of other gingers was synchronized within species, although the synchronization was far less, compared with GF species. An increase of flowering intensity in the GF period was not observed (Sakai 2000). On the other hand, flowering intensity of *Macaranga hosei* (Euphorbiaceae), categorized as a sub-annual species, increased in GF in 1992 and 1996 (Sakai et al. 1999c; Davies and Ashton 1999). Eleven sympatric *Macaranga* species have a single yearly flowering peak, and most of their reproductive activities were limited to several months within a year, except for two continuously flowering species. Their flowering periods were synchronized among species, and flowering intervals were not strictly constant. Davies and Ashton (1999) argued that these *Macaranga* species responded to a common flowering cue. An increase in flowering intensity might be related to increased irradiance levels associated with drought periods, which are likely linked with GF.

The environmental trigger of GF is still somewhat controversial. An association between GF and severe drought is often reported from different forests, and important roles of prolonged drought or increased photoperiod have been suggested repeatedly (Wood 1956; Burgress 1972; Medway 1972; Janzen 1974; Whitmore 1984; Appanah 1985; van Schaik 1986; Kiyono and Hastaniah 1999). One argument is that if reproduction is limited by photosynthesis, it is reasonable that plants may only reproduce in years when they can accumulate more energy and reserves through photosynthesis. The correlation between ENSO and GF was significant, especially in eastern Peninsular Malaysia (Ashton et al. 1988) and western Kalimantan (Curran et al. 1999; Curran and Leighton 2000), and El Niño usually brings about diminished rainfall in that region (Leighton and Wirawan 1986; Salafsky 1994; McGregor and Nieuwolt 1998).

However, there is doubt that drought itself induces flowering (Ashton et al. 1988). Such skepticism exists because correlations between flowering intensity and local geography, or water availability, have not been found. If water shortage directly induces flowering, flowering should be affected by local topography, soil types, altitudes, and so on. In addition, the relationship between rainfall seasonality and timing of a GF is obscure. For example, in eastern Peninsular Malaysia and SW Borneo the driest month is often January, although GF in eastern Peninsular Malaysia occurs from February to July, while in western Borneo it is from August through November. Ng (1977) suggested that a longer photoperiod was an alternative trigger, not affected by soils or local topography. It remains uncertain whether an increase of hours of direct sunshine, caused by less cloudiness (rather than by longer day length) can provide an effective cue for synchronized flowering of dipterocarp species, when the flowering of single tree lasts only 2 to 3.5 weeks (Ashton et al. 1988). A decrease in photoperiod by some 30 minutes is now thought sufficient stimulus to cause flower bud formation in some tropical trees (Rivera and Borchert 2001).

Apparently, Wycherley (1973) was the first to propose an abnormal temperature was the cue for GF. Based on an analysis of meteorological records for 11 years, Ashton et al. (1988) suggested this condition was a decrease in the minimum temperature. Supporting that hypothesis, reductions of minimum temperature were observed about one month before the onset of GF at Lambir in 1996 and 1997 (see Fig. 4.3), and at Pasoh Forest Reserve in Peninsular Malaysia in 1996 (Yasuda et al. 1999). However, GF occurred without a preceding temperature drop in Singapore in 1987, in Danum, Sabah, in 1987 and in Gunung Palung NP, West Kalimantan, in 1987 and 1991 (Corlett and La Frankie 1998). It is often difficult to identify the direct trigger from simple observation, because many meteorological factors, such as temperature, rainfall, humidity, and solar radiation, are closely related, and never change independently. Flowering also depends on the internal conditions of plants. Therefore, the same climatic conditions do not always bring about the same plant responses. An experimental approach is needed to evaluate the possible triggers of flower production.

4.6 Directions of Future Research

Clearly, long-term monitoring of plant phenology is more important now that global environmental change and global warming are recognized as critical issues. Climate change affects the ecosystem through plant and/or animal behavior, plant-animal interactions, and their biodiversity (Reich 1995; Corlett and LaFrankie 1998; Visser and Holleman 2000; Both and Visser 2001; Chuine and Beaubien 2001; Penuelas and Filella 2001). Harrison (2000b) reported that severe drought in 1997–98 associated with El Niño caused a substantial break in the production of inflorescences on dioecious figs and led to the local extinction of their pollinators at Lambir Hills. It brought about absences of the fig crops that were essential for the survival of mammals. The global climate change is thought to strengthen effects of El Niño and drought in the region.

At the same time, strong biological seasonality provided by GF is a very interesting and important theme to study in ecology. As we have seen, lowland dipterocarp forests with GF have a flowering phenology quite different from that in the Neotropics. The differences raise many other questions. Are there any differences in regeneration ecology of trees compared with other tropical forests? Are there fewer birds and mammals feeding on fruits and seeds in dipterocarp forests than in others? Are seed predating insects less specialized? Do supra-annual flowering plants invest in reproduction as much as annual flowering species? We do not have clear answers to these questions, and we are still at the beginning of GF studies. LaFrankie (Chapter 16) discusses the higher seedling density of canopy species in Malaysian forests compared to Neotropical forests. That, also, may be related to differences in the regeneration habit of canopy tree species, but we do not understand the mechanisms. Sakai (2002) compared mammal and bird biomass and their consumption of fruits in a Malaysian and Neotropical forest from the literature and could not find any significant difference. Moreover, because most dipterocarp seeds are dispersed by gravity and wind, the proportion of animal-dispersed plants is generally low in dipterocarp forests. Vertebrate pollinators are less common, and the diversity of nectarivorous birds is lower at Lambir than at La Selva, Costa Rica. One possible cause is that vertebrates have difficulty maintaining their populations using only floral resources. The work by Nakagawa et al. (2003) on insect seed predators of dipterocarps revealed a rather broad diet and large overlap in hosts used by different insect seed predators. More surprisingly, the dominant insect group changed dramatically among GF years. Loose pollination niches and pollinator generalization seem involved. The correlation between flowering habit and specificity of seed predators has still not been examined.

Other thematic problems are related to material cycling in the ecosystem. No studies have examined whether forests with GF, in which most large trees reproduce infrequently, produce on average less fruit or reproductive tissue, according to their biomass, than do the trees of forests dominated by sub-annual and annual flowering species. Our seed trap surveys, initiated in 2002, will provide an answer to that and other questions in the next GF event. We are ignorant of consequences from large fluctuations in the amount of input from trees to the ground, in terms of biomass, or considering the amount of carbon, nitrogen, and minerals, due to the GF cycles. Synchronized flowering of many canopy species once in several years may also change photosynthetic activities of the forest, and thus even affect Earth’s atmosphere.