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IRREGULAR DROUGHTS TRIGGER MASS FLOWERING IN ASEASONAL TROPICAL FORESTS IN ASIA¹

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General flowering is a community-wide masting phenomenon, which is thus far documented only in aseasonal tropical forests in Asia. Although the canopy and emergent layers of forests in this region are dominated by species of a single family, Dipterocarpaceae, general flowering involves various plant groups. Studying proximate factors and estimating the flowering patterns of the past and future may aid our understanding of the ecological significance and evolutionary factors behind this phenomenon. Here we show that this phenomenon is most likely triggered by irregular droughts based on 10 years of observations. In the aseasonal forests of SE Asia, droughts tend to occur during transition periods from La Niña to El Niño, which results in an irregular 6–7-yr cycle involving a dry period with several droughts and a wet period without droughts. The magnitude of a flowering event also depends on the timing of droughts associated with the El Niño southern oscillation (ENSO) cycle, with the largest events occurring after an interval of several years with no flowering. Because most plant species can only reproduce successfully during large flowering events, changes in the ENSO cycle resulting from global warming, may have serious ramifications for forest regeneration in this region.

Key words: Borneo; dipterocarp forests; Lambir; mass flowering; masting; Malaysia; phenology; Sarawak.

Masting is the intermittent production of large seed crops by a plant species synchronized within a population (Kelly, 1994). The phenomenon has attracted the attention of biologists and has been studied intensively, especially in temperate canopy tree species such as oaks and beeches. In many cases, fluctuations in fruit production are partly or mostly due to fluctuations in flower production. Although variation in flower/fruit production may be explained by resource matching (e.g., crops sizes vary simply in response to environmental variation), in most cases the fluctuation is much larger than anticipated. Thus, evolutionary factors that favor large fluctuation are thought to be involved. Promotion of wind pollination, predator satiation, and animal dispersal are often suggested as selective agents (Kelly, 1994).

General flowering (GF), one of the most spectacular and mysterious phenomena in tropical biology, is a masting phenomenon unique to Asian dipterocarp forests. It is unique in involving the synchronization of flowering thus fruiting across diverse plant groups (Ashton et al., 1988; Sakai, 2002). GF occurs at irregular intervals of less than 1 year to several years. During such an event, most dipterocarps and many other plants, from shrubs to emergent trees to epiphytic orchids,

flower over roughly a 3-mo period. Conversely, flowers are scant between GF events especially in the canopy and emergent layers, while many understory herbs and treelets may flower more frequently. The timing and extent of GF appears to be unpredictable. GF occurs in different seasons at the same sites and may be widespread, for example extending across the entire Sunda region, or it may be localized (Ashton et al., 1988). Thus, in the lowland dipterocarp forests of SE Asia, many taxa respond to the same flowering trigger, but the trigger occurs at irregular intervals, at various times of the year, and over both large and small areas. The situation is very different to that in the equatorial regions of the Americas where small annual changes in sunrise and sunset trigger flowering and leaf flushing (Borchert et al., 2005).

Several hypotheses for the evolution of GF have been proposed, including the most widely accepted one of seed predator satiation. Recently, two groups (Sakai, 2002; Williamson and Ickes, 2002) have independently suggested the potential role of “environmental prediction” in the evolution of GF. They hypothesize that plants can predict which years will be best for the survival of seedlings, then synchronously flower and produce seeds only in such years. While the hypothesis may not hold true for masting in seasonal climates, except for some special cases (Kelly, 1994), it may be more significant in aseasonal climates. In seasonal climates, most flowering triggers of annually flowering plants cause not only synchronization among individuals, but also signal the start of a new climatic condition or season. For example, heavy rain after a long dry period induces the flowering of tropical shrubs, and the rain also indicates the start of wet conditions lasting for several months (Augspurger, 1981). Many temperate woody species flower at the same time of the year in response to temperature or cumulative heatsums (Rathcke

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and Lacey, 1985). Because the climate has an annual cycle, plants can anticipate climatic conditions at least in terms of annual averages. On the other hand, whether flowering triggers also signal some future climatic condition and whether plants have evolved to flower in favorable periods for pollination or the establishment of seedlings in aseasonal climates, often with more prominent supra-annual rhythms than annual ones, have rarely been investigated.

Proximate factors of general flowering have been the subject of controversy over the last decades. Identification of the trigger is considered to be important for evaluating roles of climatic conditions as a determinant of phenology, and to assess why community-wide masting phenomenon does not occur in other tropical regions. In addition, such information is essential for the management and conservation of an endangered ecosystem, especially to explore effects of climate changes on forest regeneration. Two climatic factors have been proposed as GF triggers: drought and a temperature drop, both of which may be associated with the El Niño Southern Oscillation (ENSO) (Ashton et al., 1988; Yasuda et al., 1999; Curran et al., 1999; Wich and van Schaik, 2000; Sakai, 2002). Prolonged droughts (e.g., Appanah, 1985) or an increase in solar radiation associated with dry conditions (Ng, 1977; van Schaik, 1986) have repeatedly been reported for GF years. On the other hand, Ashton et al. (1988) argued, based on 11-yr records of flowering from Pasoh, Malay Peninsula, that a drop in the daily minimum temperature always preceded flowering events. Temperature drops preceding GF were also confirmed for later flowering events at that site (Yasuda et al., 1999; Numata et al., 2003) and other sites (Sakai et al., 1999). Many of these researchers presented data from single environmental cues and GF records or only casually mentioned an association. Yasuda et al. (1999) and Numata et al. (2003) examined temperature and rainfall in parallel, but as they discussed, there was a correlation between the two climatic variables, which prevented distinguishing between the two hypotheses.

In this paper, we examine GF triggers based on observations over a 10-yr period, comprising four GF years. We also present temporal patterns of flowering triggers over a period of 19 yr and meteorological conditions associated with the triggers. Finally, we discuss hypotheses for the evolution of GF in the light of meteorological characteristics of the identified triggers.

MATERIALS AND METHODS

Study site—Our study was carried out in a lowland dipterocarp forest at Lambir Hills National Park, Borneo (4°20'N, 113°50'E, 150–250 m above sea level) (Roubik et al., 2005). Rainfall data were collected at the Bukit Lambir Station of the Department of Irrigation and Drainage (DID), Sarawak, Malaysia, within the park approximately 3 km northwest of the study site. From 1985–2003, the average annual rainfall was 2722 mm and ranged from 2044 mm to 3822 mm. Seasonal variation was significant but low, and the area occasionally had droughts with biological consequences (Harrison, 2000; Nakagawa et al., 2000; Delissio, 2003; Potts, 2003; Iitoka and Yamauti, 2004).

Plants were observed using a canopy observation system (tree towers and walkways) constructed at the center of the Canopy Biology Plot (8 ha, 200 × 400 m) (Roubik et al., 2005) and another tree tower constructed as a tourist attraction. The Canopy Biology Plot includes humult and uduft soils (sandy clay, light clay, or heavy clay in texture), several ridges and valleys, and closed (mature-stage) forests and canopy gaps. The tower for tourists is situated along a stream on yellow sandstone, 2 km northeast of the Canopy Biology Plot. Because the plant reproductive phenology did not differ significantly between the two sites, we treated them together throughout this paper.

Meteorological data—We calculated the 30-d moving rainfall total to identify droughts (defined as <40 mm total rainfall for more than 30 d). Meteorological rhythms in the tropical part of the Indian monsoon area (Asia, Australia, and the West Pacific) tend to generate dry spells of 15–30 days (Yasunari, 1979), and hence a 30-d period best links flowering patterns to the occurrence of drought. From 1993 to 1998, temperature was monitored every 30 min (temperature/humidity sensor, E7050–10, Yakogawa Weathac Corp., Tokyo, Japan) from a tower 35 m above the ground located at our study site, and since 2000 every 10 min on a different tower 50 m above the ground (VHE-Z23, Vaisala K. K., and Hobo H8Pro, Onset). Also in 2000, a solar radiometer (MS401, EKO, Tokyo, Japan) was installed on the top of a canopy crane 85.8 m above the ground. Readings were taken every 5 s and averaged over 10 min (CR10X data logger, Campbell Scientific, Logan, Utah, USA). Both temperature and radiation data sets have missing values due to mechanical problems.

Because droughts are known to be associated with ENSO in this region, we examined the relationship of droughts from 1985–2003 at Lambir Hills and the Troup southern oscillation index (SOI), which is the standardized anomaly of the difference in mean sea level pressure between Tahiti and Darwin. Sustained negative values of the SOI indicate El Niño episodes.

Monitoring plant reproduction—We have monitored reproductive activities of trees, lianas, and epiphytes since 1993 (Sakai et al., 1999). Our sampling of the plants did not directly reflect the number of individuals of each life form, but was weighted toward larger plants (i.e., canopy and emergent trees). Due to the death of some of the monitored plants and an incomplete data set, we used data from 309 individuals of 178 species for this study, including 114 dipterocarps of 40 species (Appendix S1, see Supplemental Data accompanying online version of this article). Flowering phenology in the GF of 1996, 1997, and 1998 of three dipterocarp genera, *Dipterocarpus* ($N = 26$), *Dryobalanops* ($N = 15$), and *Shorea* ($N = 67$), and two other families, Burseraceae ($N = 17$) and Euphorbiaceae ($N = 34$), were compared to examine the correlation between meteorological factors and flowering patterns. Flowering in 2001 was not shown because the flowering sequences were not clear, probably due to successive flowering triggers within a short period.

Plant phenology was monitored twice a month and, in this paper, we report results from July 1993 up to the end of September 2003. At each census, reproductive organs (flower buds, flowers, and fruits) were observed, and the intensity of reproductive activity for each individual was recorded as one of five grades: 0, nonreproductive; +, very few flowers or fruits covering <1% of the crown; 1, >1% and <50% of the crown covered with flowers or fruits; 2, >50% and <80% of the crown covered with flowers or fruits; 3, flowers or fruits covering >80% of the crown.

Flowering and fruit set of Dipterocarpaceae in different years—For dipterocarps, we define a reproductive event as a series of plant reproductive activities from flowering to fruit dispersal. Indices of flowering and fruiting were determined as the maximum grade of intensity of plant reproductive activities, as defined earlier, throughout the period with flowers and mature fruits, respectively. Therefore, these two variables (e.g., indices of flowering and fruiting) were divided into four categories (+, 1, 2, and 3, as described). Very minor reproductive events in which the maximum grade of the intensity of reproductive activities throughout the event was +, usually indicating the flowering of only one branchlet on a large tree, were excluded from the following analysis.

We classified the events based on the year when the event started (the first date of observed flowering or fruiting). Reproductive events in 1993 and 2003 were excluded from the analysis due to incomplete coverage in those years. We defined an index of the magnitude of GF (1, 2, and 3) based on the number of reproductive events for Dipterocarpaceae in each year (see Results), rather than all reproductive events. This was done because the flowering phenology of Dipterocarpaceae showed the strongest association with GF (Sakai et al., 1999), and because reproductive events of Dipterocarpaceae could be more clearly identified. In taxa with very short reproductive events or, conversely, those that are flowering or fruiting most of the time, it can be difficult to distinguish reproductive events. To evaluate relationships among the three variables (magnitude of GF, intensity of flowering, and intensity of fruiting), we calculated the Spearman correlation coefficients for all paired combinations. Because there were correlations between all three variables, we further evaluated the correlation between the magnitude of GF and the fruit set by calculating the Spearman partial correlation coefficients for the magnitude of GF and the intensity of fruiting controlled by the intensity of flowering. Then

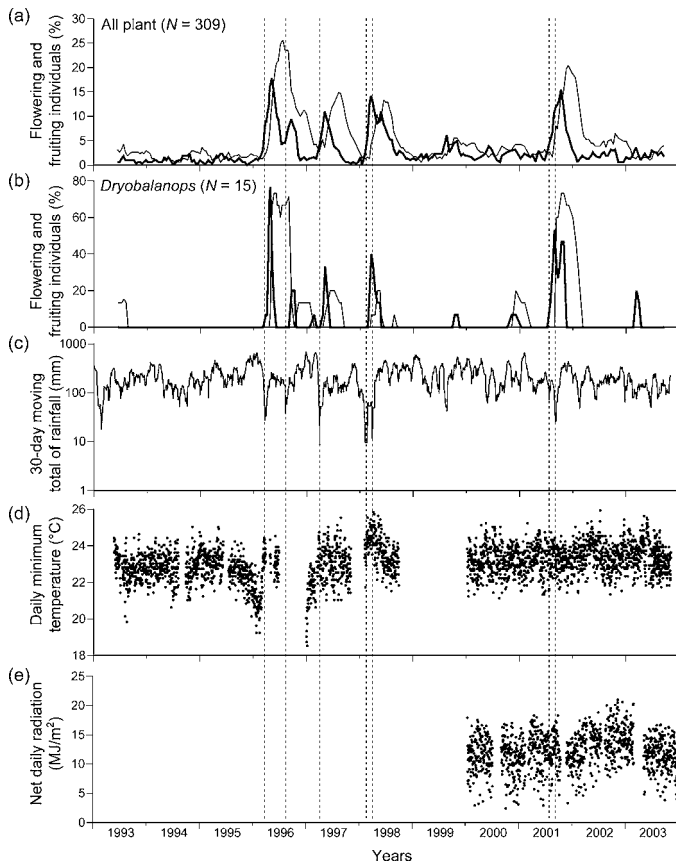


Fig. 1. Plant reproductive phenology and climatic variables over 10 yrs at Lambir Hills National Park, Sarawak, Malaysia. Vertical dotted lines indicate the timing of drought peaks. (a) Temporal changes in the proportion of flowering (thick line) and fruiting (thin line) in all individuals monitored in this study (see Appendix S1 in Supplemental Data with online version of this article; $N = 309$). (b) Changes in the proportion of flowering (thick line) and fruiting (thin line) individuals of *Dryobalanops aromatica* and *D. lanceolata* (Dipterocarpaceae) ($N = 15$). (c) Changes in total rainfall over the preceding 30-d period. The horizontal line indicates 40 mm, the maximum rainfall for our definition of drought. (d) Daily minimum temperature monitored on top of tree towers at our study site. (e) Daily changes in average net daily radiation over 10-d and monitored from the top terrace of a canopy crane.

we tested if the coefficients deviated significantly from zero. The analysis was conducted using program SAS (SAS Institute, Cary, North Carolina, USA).

RESULTS

Flowering patterns and meteorological data—During the 10 years, we observed a relatively large GF in 1996 and small GFs in 1997, 1998, and 2001 (Fig. 1). GF in 1996 clearly had two peaks, and in each peak, the composition and sequence of flowering species were similar. Two flowering peaks, with considerable overlap, could also be discerned in 1998 and in 2001 (Fig. 1).

A close association between temperature drops and droughts was not observed. Significant temperature drops preceded GF in 1996 and 1997, by 3 and 4 months, respectively (Fig. 1d). However, no temperature drop was observed in 2001. On the other hand, on every occasion that the 30-day total rainfall

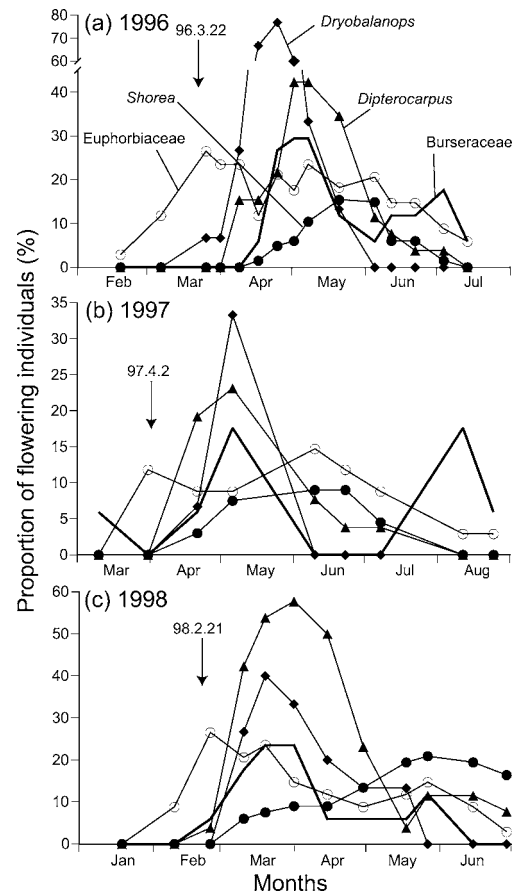


Fig. 2. Changes in the proportion of flowering individuals in three genera *Dipterocarpus* ($N = 26$), *Dryobalanops* ($N = 15$), and *Shorea* ($N = 67$) (Dipterocarpaceae), and the two families Burseraceae ($N = 17$) and Euphorbiaceae ($N = 17$) over three general flowering events in 1996 (a), 1997 (b), and 1998 (c). The arrow indicates the timing of the drought in each case.

dropped below 40 mm, either a small or a large GF occurred (Fig. 1c). All flowering peaks were also preceded by a drought, with one exception. In 2001, two rather indistinct flowering peaks were observed, but only one drought (30 day rainfall total < 40 mm) was recorded. However, an additional dry spell (30 day rainfall total = 70.5 mm) did occur 1.5 months before flowering. Fluctuations in radiation are roughly correlated with rainfall patterns (Fig. 1e). However, in 2001 three peaks of solar radiation of similar strength were observed, but only the last one was followed by a relatively large flowering. Therefore, the strength of radiation and the magnitude of flowering did not correlate well, and the temporal match of increased radiation with the onset of flowering was variable. From these results, we concluded that drought is the most plausible trigger of GF.

Close examination revealed a very constant temporal relationship between the timing of droughts and flowering (Fig. 2). The interval between a drought and flowering was very short. In 1996, the first observed flowering of *Dryobalanops* was recorded on 26 March, 4 days after the end of a drought. In 2001, *Dryobalanops* was observed flowering on July 31, 10 days after the end of the minor drought mentioned. Flowering sequences in the four GFs of 1996, 1997, and 1998 did not vary significantly. Euphorbia-

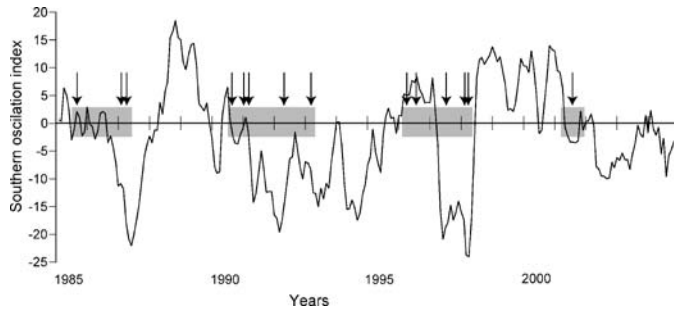


Fig. 3. Occurrence of droughts (30-d rainfall total < 40 mm) (arrows) and the 3-mo moving average of the southern oscillation index (SOI). Dry periods with droughts are shaded. Negative SOI values indicate El Niño conditions.

ceae usually started flowering well before other groups, and flowering peaked when the 30-day total rainfall was lowest or when the drought ended (Fig. 2, indicated by arrows). About 1 month after the end of a drought, flowering peaks were recorded for *Dryobalanops*, *Dipterocarpus*, and *Burseraceae*. In all 3 years, *Burseraceae* had two flowering peaks; the two peaks included both some of the same and some different species. *Shorea* always flowered last.

Nineteen-year southern oscillation index and drought records—From 1985 to 2003, droughts (measured as total rainfall < 40 mm for 30 d) occurred 14 times (Fig. 3): three from 1985–1988, five from 1990–1993, and five from 1996–1998. Droughts most often occurred when the SOI was changing from positive to negative, indicating transition periods from La Niña to El Niño.

Magnitude of fruiting—From 1994 to 2002, 269 dipterocarp reproductive events were recorded. The numbers of reproductive events in 1996, 1997, 1998, and 2001 were 82, 45, 59, and 57, respectively. In other years, there were six events or less. Thus, three categories for GF year were determined: 1, non-GF years (1994, 1995, 1999, 2000, and 2002); 2, small-GF years (1997, 1998, and 2001); and 3, large-GF year (1996) (Fig. 4). The three variables (e.g., category of GF year, intensity of flowering, and intensity of fruiting) were significantly correlated (category of GF year and flowering, $P = 0.001$; category of GF year and fruiting, $P < 0.001$; flowering and fruiting, $P < 0.001$). The partial correlation between category of GF year and fruiting intensity controlled by flowering intensity was both positive and highly significant ($r = 0.162$, $P = 0.008$).

DISCUSSION

Trigger of general flowering—From our studies in Borneo over a 10-yr period, we conclude that drought is the most plausible trigger for GF. We recorded a large GF in 1996 and smaller flowering events in late 1997, 1998, and 2001 (Fig. 1). All flowering peaks were preceded by dry periods, except one in 2001 preceded by a weak dry spell (discussed in the next section), and every drought (30-d rainfall total < 40 mm, see Materials and Methods section) was followed by a flowering. The different plant taxa examined had a similar sequence of flowering in different GF events, supporting the view that they are responding to a common trigger. A previous study among

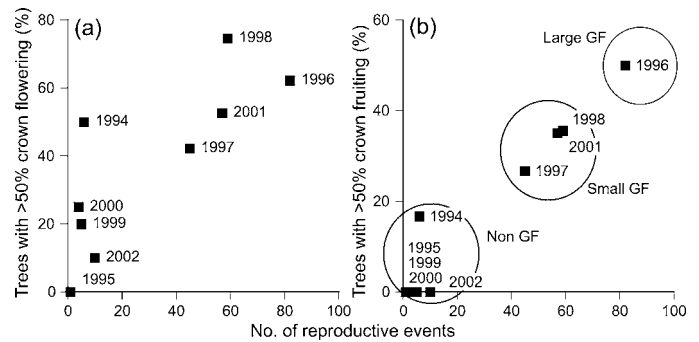


Fig. 4. Proportion of flowering trees with over 50% of crown (a) flowering and (b) fruiting in different years from 1994 to 2002 plotted against the total number of dipterocarps flowering over the year. The numbers of trees flowering in 1996, 1997, 1998, and 2001 were 82, 45, 59, and 57, respectively. In other years, fewer than six trees flowered. Thus, the years were categorized into three general flowering categories; high (1996), low (1997, 1998, and 2001), and non-general flowering (1994, 1995, 1999, 2000, and 2002).

Shorea species on the Malay Peninsular also confirmed similar flowering sequences in different flowering events (LaFrankie and Chan, 1991). Interestingly, minor droughts were found to trigger leaf flushing in several species (Ichie et al., 2004). Flower induction is basically the transformation of leaf buds to flower buds (Syamuswida and Owen, 1997). Thus, these results suggest plants initiate buds when dry conditions start and produce either leaves or flowers depending on the severity of the drought. Conversely, neither temperature nor solar radiation was clearly correlated with flowering. Although our temperature data have some gaps and temperature drop cannot be examined in some years, we can safely say that GF can occur without a preceding drop in temperature as shown by the flowering in 2001. For solar radiation, however, we may need further data and analysis to evaluate its role as a flowering trigger because data are available for only a relatively short period.

One of the subjects for future studies is how the plants respond to the drought so quickly. Some species start flowering before the peak of the drought (Fig. 2). Because the end of the drought is actually the start of rainfall, the observed pattern indicates that at least some of the plants start flowering in response to drought rather than to the rain after the drought. Nevertheless, the interval between the start of drought and that of flowering is still shorter than the time usually required for flower development in many other plants (Salisbury, 1963). Careful anatomical observation of flower development may be required before we conclude that drought is a sufficient condition for flower initiation (Syamuswida and Owens, 1997).

Dry conditions in SE Asia are associated with the El Niño cycle (Popelewski and Halpert, 1987). From 1985 to 2003, the 14 droughts fell into three periods from 1985 to 1988, from 1990 to 1993, and from 1996 to 1998. There may be an irregular 6–7-yr cycle involving a dry period with several droughts and a wet period without droughts. Droughts occurred during transition periods from the La Niña to El Niño, or at the beginning of an El Niño period. The five droughts associated with the 1996–1998 period triggered four successive flowerings in three years and similar patterns have been reported from other sites (Yap and Chan, 1990; Curran et al., 1999). Because of the dry–wet cycles, flowering intervals are very irregular, and earlier studies have tended to overlook the shorter intervals (e.g., Janzen, 1974).

Magnitude of flowering and fruiting—Correlation between the strength of a drought and the magnitude of a GF event does not seem to be very simple. The magnitude may be affected by the level of accumulated resources in addition to the strength of the trigger. During the 1996–1998 period, the first flowering episode in 1996 was much bigger than the subsequent flowerings. Stored phosphorus, rather than carbon or nitrogen, may be a determinant of the magnitude because it is known that phosphorus in dipterocarp trees dramatically decrease during flowering and fruiting (T. Ichie, Kochi University, personal communication). The level of accumulated resources may also affect the response threshold to the trigger. For example, the first of two flowering peaks in 2001, which occurred after 3 years without flowering, was preceded by a relatively weak dry period (30-d rainfall total = 70.5 mm). We think that a relatively long wet period before the drought increases the sensitivity of the plant to the trigger.

Magnitude of GF may strongly affect reproductive success of individual trees. In our study, many individual trees produced a large number of flowers in both small and large flowering events, but fruit crops were smaller in small GF events (Fig. 4). The partial correlation between the category of GF year and flowering intensity was positive and significant ($P = 0.008$), meaning that more large-flowering events resulted in large fruit crops during a big GF year than in smaller GF years. These results could be explained by either increased pollination success (outcrossing opportunities or pollinator facilitation) or increased pre-dispersal seed survival during larger flowering events or a combination of both factors. In several studies, increased postdispersal seed and seedling survival during larger flowering events has also been demonstrated (Curran and Leighton, 2000). Only the first flowering event of a wet period may contribute to regeneration of GF plants.

Implications to evolutionary factors—The most parsimonious explanation of general flowering is simply the irregular occurrence of the flowering trigger. For most of their evolutionary history, the lowland dipterocarp forests of SE Asia have experienced a drier, more seasonal climate (Ashton et al., 1988). Today, flowering normally occurs toward the end of the dry season or beginning of the wet season in seasonal forests in Asia. Hence, it is not unreasonable to suggest that at the onset of humid, aseasonal conditions 7000 years ago, species were physiologically committed to waiting for a dry-season trigger, thus irregular occurrences of drought has led to the GF phenomenon. This historically based hypothesis would also explain why GF is a community-wide phenomenon, affecting many different taxa and ecological types, which would be a surprising result for most of the other hypotheses. Nevertheless, one or more selective factors, such as seed predator satiation, pollination facilitation and/or environmental prediction, are believed to have played a role in the evolution of GF because of such strong synchronization of reproduction among various plant species.

Association among flowering trigger, magnitude of fruiting, and ENSO revealed by this study has important implications for understanding the evolutionary factors behind GF. For example, it has been postulated that the onset of rain following a drought should indicate the start of a long wet period before the next drought, and hence more seedlings will survive (Sakai, 2002). However, this is clearly not the case when droughts in successive years are common, and the first flowering event in a series usually results in successful mass fruiting (see the

previous section). On the other hand, droughts or clear weather may be favorable for pollination and accumulation of resources for reproduction (van Schaik et al., 1993). The current photosynthates, rather than stored assimilates, are considered to be the major carbon source for fruit development in dipterocarp trees (Ichie et al., 2005). Williamson and Ickes (2002) proposed that droughts that trigger flowering provide a favorable environment for seedling recruitment by improving light conditions on the forest floor because the drought also caused substantial defoliation and mortality of canopy trees. On the other hand, repetition of consecutive masting and nonflowering periods suggests that the resource matching hypothesis (Kelly, 1994) and the strict resource threshold model (Isagi et al., 1997) do not explain the timing of GF events. GF, when we do not consider variations in magnitude, seems to be governed by triggers rather than resources.

By far the most popular hypothesis proposed to explain GF is that of “seed predator satiation” (Janzen, 1974; Curran et al., 1999; Curran and Leighton, 2000): Populations of seed predators are reduced during periods of low seed production, so that in a masting the seed predator population is quickly satiated and a high proportion of seeds escape. As applied to GF, the hypothesis assumes that the interval between flowerings is long, so that the high populations of seed predators generated during one masting event decline before the next. The hypothesis is supported by a decline in viable seed and seedling establishment during a minor flowering event compared with that during a major event (Curran and Leighton, 2000). The present study suggests, however, that in addition to the magnitude of fruiting, the intervals between flowerings may also influence the effectiveness of seed predator satiation because the length of the time intervals are highly variable. Further studies on the intensity of fruiting, population dynamics of seed predators, and survival of seeds and seedlings are needed to understand efficiency of predator satiation in GF.

Implications for conservation—A recent increase in the intensity and frequency of droughts has been reported for several places in Borneo (Harrison, 2005) and other tropical regions (Condit, 1998). This may be due to global climate change (Timmermann et al., 1999), a decrease in forest cover, or long-term periodic changes in ENSO frequency and magnitude. However, the effect of these changes on the ecology of dipterocarp forests is unknown (Corlett and LaFrankie, 1998). ENSO-related droughts are thought to have occurred in Borneo throughout the Late Pleistocene and Holocene periods, but estimates of the frequency and magnitude have varied considerably. From 15 000 to 7000 yr BP ENSO is thought to have had a cycle of about 15 yr, while it is 2–8.5 yr at present (Robell et al., 1999). There have also been substantial changes in the extent of lowland forests in SE Asia, as a result of sea-level fluctuations, and their seasonality. Changes in drought frequency and magnitude may have serious consequences for the long-term viability of these forests, although it may not be very apparent at the moment, especially in the face of other anthropogenic changes such as deforestation. For example, the results of this study suggest that changes in the ENSO cycle, may have serious ramifications for forest regeneration in this region, because most plant species can only reproduce successfully during large flowering events after wet periods for several years. A greater effort should be made to coordinate studies among sites to further the understanding the GF phenomenon.

LITERATURE CITED

- APPANAH, S. 1985. General flowering in the climax rain forests of Southeast Asia. *Journal of Tropical Ecology* 1: 225–40.
- ASHTON, P. S., T. J. GIVNISH, AND S. APPANAH. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132: 44–66.
- AUGSPURGER, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinator and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775–788.
- BORCHERT, R., S. S. RENNER, Z. CALLE, D. NAVARRETE, A. TYE, L. GAUTLIER, R. SPICHIGER, AND P. VON HILDEBRAND. 2005. Photoperiodic induction of synchronous flowering near the equator. *Nature* 433: 627–629.
- CONDIT, R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change* 39: 413–427.
- CORLETT, R. T., AND J. V. LAFRANKIE. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climate Change* 39: 317–336.
- CURRAN, L. M., I. CANIAGO, G. D. PAOLI, D. ASTIANI, M. KUSNETI, M. LEIGHTON, C. E. NIRARITA, AND H. HAERUMAN. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286: 2184–2188.
- CURRAN, L. M., AND M. LEIGHTON. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70: 101–128.
- DELISSIO, L. J., AND R. B. PRIMACK. 2003. The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology* 19: 489–500.
- HARRISON, R. D. 2000. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London, B, Biological Sciences* 267: 911–915.
- HARRISON, R. D. 2005. A severe drought in Lambir Hills National Park. In R. D. Roubik, S. Sakai, and A. A. Hamid [eds.], *Pollination ecology and the rainforest: Sarawak studies*, 51–64. Springer, New York, New York, USA.
- ICHIE, T., T. HIROMI, R. YONEDA, K. KAMIYA, M. KOHIRA, I. NINOMIYA, AND K. OGINO. 2004. Short-term drought causes synchronous leaf shedding and flushing in a lowland mixed dipterocarp forest, Sarawak, Malaysia. *Journal of Tropical Ecology* 20: 267–700.
- ICHIE, T., T. KENZO, Y. KITAHASHI, T. KOIKE, AND T. NAKASHIZUKA. 2005. How does *Dryobalanops aromatica* supply carbohydrate resources for reproduction in a masting year? *Trees* 19: 703–710.
- ISAGI, Y., K. SUGIMURA, A. SUMIDA, AND H. ITO. 1997. How does masting happen and synchronize? *Journal of Theoretical Biology* 187: 231–239.
- ITIOKA, T., AND M. YAMAUTI. 2004. Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. *Journal of Tropical Ecology* 20: 479–482.
- JANZEN, D. H. 1974. Tropical blackwater rivers, animals and mast flowering by the Dipterocarpaceae. *Biotropica* 6: 69–103.
- KELLY, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9: 465–470.
- LAFRANKIE, J. V., AND H. T. CHAN. 1991. Confirmation of sequential flowering in *Shorea* (Dipterocarpaceae). *Biotropica* 23: 200–203.
- NAKAGAWA, M., K. TANAKA, T. NAKASHIZUKA, T. OHKUBO, T. KATO, T. MAEDA, K. SATO, H. MIGUCHI, H. NAGAMASU, K. OGINO, S. TEO, A. A. HAMID, AND H. S. LEE. 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16: 355–367.
- NG, F. S. P. 1977. Gregarious flowering of dipterocarps in Kepong (1976). *Malaysian Forester* 40: 126–136.
- NUMATA, S., M. YASUDA, T. OKUDA, N. KACHI, AND N. S. MD. NOOR. 2003. Temporal and spatial patterns of mass flowerings on the Malay Peninsula. *American Journal of Botany* 90: 1025–1031.
- POPELEWSKI, C. F., AND M. S. HALPERT. 1987. Global and regional scale precipitation patterns associated with the El Niño southern oscillation. *Monthly Weather Review* 115: 1606–1625.
- POTTS, M. D. 2003. Drought in a Bornean everwet rain forest. *Journal of Ecology* 91: 467–474.
- RATCHE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.
- ROBELL, D. T., G. O. SELTZER, D. M. ANDERSON, M. B. ABBOT, D. B. ENFIELD, AND J. H. NEWMAN. 1999. An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. *Science* 283: 516–520.
- ROUBIK, R. D., S. SAKAI, AND A. A. HAMID. 2005. *Pollination ecology and the rainforest: Sarawak studies*. Springer, New York, New York, USA.
- SAKAI, S. 2002. General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biological Journal of Linnean Society* 75: 223–247.
- SAKAI, S., K. MOMOSE, T. YUMOTO, T. NAGAMITSU, H. NAGAMASU, A. A. HAMID, T. NAKASHIZUKA, AND T. INOUE. 1999. Plant reproductive phenology over four years including an episode of GF in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* 86: 1414–1436.
- SALISBURY, F. B. 1963. *The flowering process*. Pergamon Press, Oxford, UK.
- SYAMSWIDA, D., AND J. N. OWENS. 1997. Time and method of floral initiation and effect of paclobutrazol on flower and fruit development in *Shorea stenoptera* (Dipterocarpaceae). *Tree Physiology* 17: 211–219.
- TIMMERMANN, A., J. OBERHURBER, M. BACHER, M. LATIF, AND E. ROECKNER. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398: 694–697.
- VAN SCHAİK, C. P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* 2: 327–47.
- VAN SCHAİK, C. P. V., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353–377.
- WICH, S. A., AND C. P. V. VAN SCHAİK. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16: 563–577.
- WILLIAMSON, G. B., AND K. ICKES. 2002. Mast fruiting and ENSO cycles—does the cue betray a cause? *Oikos* 97: 459–460.
- YAP, S. K., AND H. T. CHAN. 1990. Phenological behavior of some *Shorea* species in Peninsular Malaysia. In K. S. Bawa and M. Hadley [eds.], *Reproductive ecology of tropical forest plants*, 21–35. UNESCO, Paris and Parthenon Publishing Group, Lancs, UK.
- YASUDA, M., J. MATSUMOTO, N. OSADA, S. E. ICHIKAWA, N. KACHI, M. TANI, T. OKUDA, A. FURUKAWA, A. R. NIK, AND N. MANOKARAN. 1999. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* 15: 437–449.
- YASUNARI, T. 1979. Cloudiness fluctuations associated with the Northern hemisphere summer monsoon. *Journal of Meteorological Society of Japan* 57: 227–242.