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STAGGERED FLOWERING IN THE DIPTEROCARPACEAE:
NEW INSIGHTS INTO FLORAL INDUCTION AND
THE EVOLUTION OF MAST FRUITING
IN THE ASEASONAL TROPICS

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Members of the family Dipterocarpaceae dominate many of the species-rich, lowland tropical rain forests of aseasonal western Malesia, a region that lacks a regular annual dry season (mean monthly rainfall less than 100 mm) and encompasses much of peninsular Malaysia, Sumatra, Java, Borneo, and the Philippines (Ashton 1964, 1982; Whitmore 1984). In the richest of these forests, dipterocarps may account for up to 10% of all tree species and 80% of all emergent individuals (Ashton 1982). Dipterocarps also occur in seasonal tropical forests and savannas in southeastern Asia, India, Sri Lanka, Madagascar, Africa, and the Guayana Highlands (fig. 1).

A striking feature of dipterocarp forests in aseasonal Malesia is the phenomenon of mass flowering, followed by mast fruiting (Ridley 1901; Foxworthy 1932; Wood 1956; McClure 1966; Medway 1972; Janzen 1974; Cockburn 1975; Chan 1977; Chan and Appanah 1980; Ashton 1982, in press). At irregular intervals of 2 to 10 years several species of dipterocarps, as well as some canopy members of such families as the Burseraceae, Fabaceae, Myristicaceae, Polygalaceae, and Sapotaceae, come into flower more or less simultaneously. Over a period lasting a few weeks to a few months, nearly all dipterocarps and up to 88% of all canopy species can flower after years of little or no reproductive activity (Medway 1972; Appanah 1979, 1981). The region over which such a mass-flowering event occurs can be as small as a single river valley or as large as northeastern Borneo or peninsular Malaysia. Enormous numbers of seeds and fruit ripen after a mass flowering and are released onto the forest floor; individual dipterocarps present up to four million flowers, from which up to 120,000 fruits may be set (Ashton, in press).

Janzen (1974) has suggested that such regionally synchronized, mast fruiting at irregular intervals of more than one year (hereafter, multi-year intervals) is an effective means of swamping seed predators, particularly in unproductive habitats that support low densities of such predators during the long intervals between

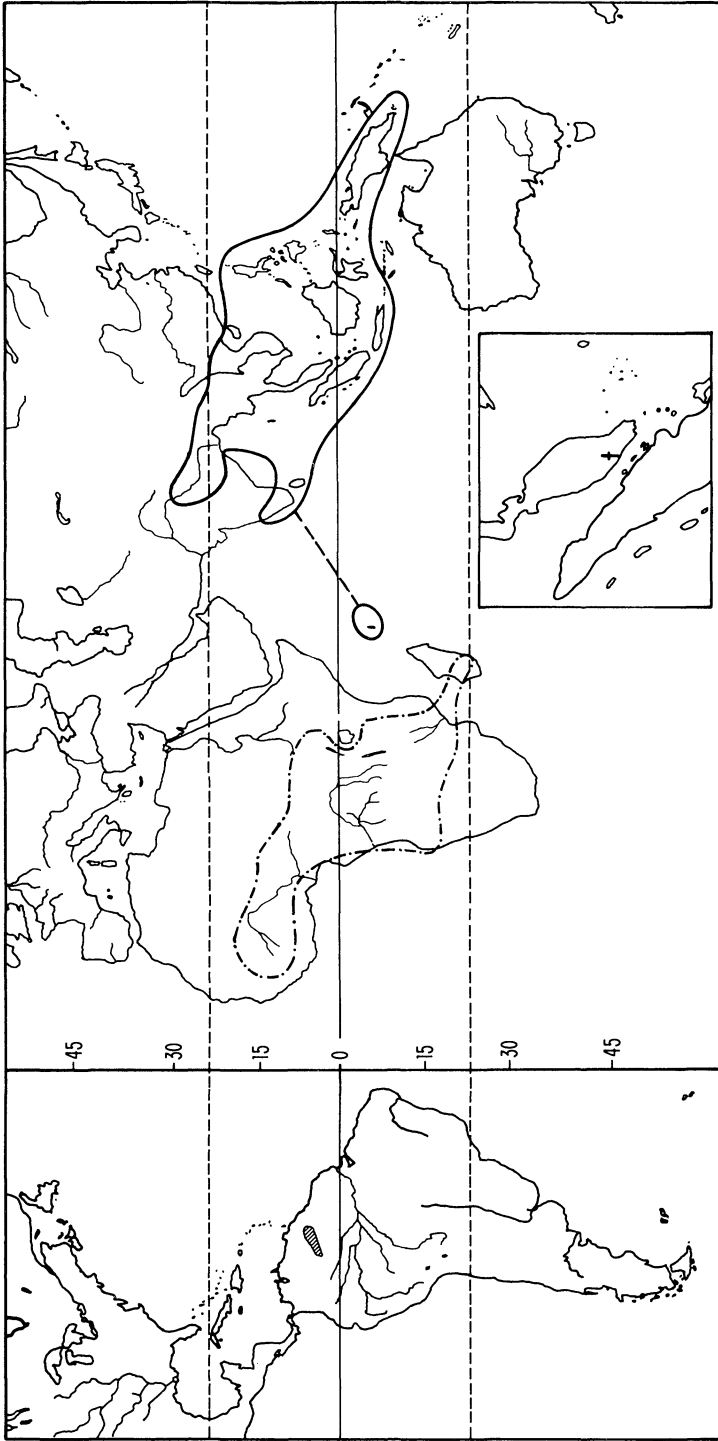


FIG. 1.—Global distribution of the family Dipterothripidae. Each continent bears a different subfamily. *Inset*, Map of peninsular Malaysia, indicating the location of the Pasoh Forest Reserve.

fruiting events. According to his scenario, species should be selected to store energy over a long period and then reproduce in synchrony with several other species in order to satiate or avoid seed predators.

The predator-satiation hypothesis seems a plausible explanation for the evolution of mast fruiting. Dipterocarp seeds are large, energy-rich, and chemically poorly protected; they are eaten voraciously by wild pigs and heavily parasitized by weevils (Chan 1977; Ashton 1982). The seedlings themselves are resinous and experience rather little predation (Daljeet Singh 1975; Becker 1983). Individuals that fruit out of synchrony suffer high levels of seed mortality (Burgess 1972). Further, dipterocarps have winged seeds and do not depend for dispersal on animals whose density would be adversely affected by mast fruiting.

Nevertheless, four key questions arise regarding how mast fruiting could evolve in dipterocarps via the proposed mechanism. (1) What pollinates species that flower at multi-year intervals, given that there are few floral resources to sustain potential pollinators during the interim? (2) How do mass-flowering tree species avoid competition for pollinators? (3) What is the environmental cue for floral induction that induces scores of species in several families to flower at irregular, multi-year intervals in an aseasonal climate? (4) And, most important, what factors could cause an initial phenological aggregation of species' fruiting times? In order for the predator-satiation hypothesis to work in species-rich forests lacking single-species dominance and for there to be any advantage to fruiting at one time versus another, there must be times when many more species (and thus many more individuals) fruit than at any other time. Once such a phenological core of species exists, selection can entrain other species into the same fruiting schedule and perfect the synchrony of seed release. The essential question is how such a phenological core of species, flowering at irregular intervals in an aseasonal climate, could initially arise.

As we attempt to demonstrate, the answers to these four questions are inter-related and cast new light on the origin of the dipterocarps, the evolution of mast fruiting, and the relation of mast fruiting to the El Niño–Southern Oscillation phenomenon.

I. WHAT POLLINATES MAST-FRUITING DIPTEROCARPS?

The crucial question of what pollinates mast-fruiting dipterocarps has, unlike the other three, already been answered (Chan 1977, 1981; Appanah 1979, 1981, 1987); we briefly review the earlier findings here. In 1976, an intensive study was conducted of the pollination biology of several dipterocarps in a mass flowering then under way in Pasoh Forest Reserve in western peninsular Malaysia (fig. 1). The principal subjects of the study were six co-occurring, closely related species of *Shorea* section *Mutica*, of a total of seven species in this section native to mixed-dipterocarp forests in Malaya.

Flowers of each species are small (roughly 1–1.5 cm in length), cream-colored, and bell-shaped at anthesis, with the anthers loosely imprisoned by a portcullis of reflexed staminal appendages beyond which the style extrudes. Flower buds are tightly contorted and present for 2 wk or more before anthesis. Individual flowers

TABLE 1
FLOWERING PERIODS FOR *SHOREA* SECTION *MUTICA* AT PASOH FOREST RESERVE, 1976

SPECIES	POPULATION FLOWERING DATE		LENGTH OF FLOWERING (days)
	First	Last	
<i>S. macroptera</i>	3/14	3/29	16
<i>S. dasyphylla</i>	3/21	4/5	16
<i>S. lepidota</i>	3/29	4/14	17
<i>S. parvifolia</i>	4/9	4/30	22
<i>S. acuminata</i>	4/18	5/10	23
<i>S. leprosula</i>	5/3	5/28	26

on an inflorescence open at dusk and emit a penetrating, sickeningly sweet smell, with the corollas dropping to the forest floor the next day. Over a million blossoms may be presented on a single night by an individual in peak bloom. Species' flowering periods range from roughly 2 to 3.5 wk, staggered over an 11-wk flowering season (table 1). All species come into fruit in tight synchrony over a 10-day period.

The *Shorea* species in question are highly self-incompatible, and their pollen is sticky and not significantly dislodged by wind. Their principal pollinators are thrips (Thysanoptera), with two species of the genus *Thrips* and one of *Lemurothrips* accounting for over 95% of the floral visitors; thrip visitation patterns do not differ significantly among *Shorea* species. Adult thrips visit open flowers to feed on pollen, rest, and oviposit on unopened flower buds. Their bodies are covered with pollen and come into intimate contact with the stigmatic surfaces. The nymphs feed on petals and sepals of the buds, rasping minute holes in these tissues. Thrips are minute and exceedingly weak flyers: movement between tree crowns and cross-pollination appear to result from the thrips drifting to the ground on shed corollas and then being deflected by air currents as they ascend to the pale, heavily scented flowers the following evening.

Thrips appear to be ideal animal pollinators for mast-fruiting species: they have a generation time of 8 days and an average fecundity of 27 eggs per female, and they can rapidly increase from the low numbers sustained between mass flowerings by feeding on scattered flowers of several understory species—such as *Randia scortechinii* King (Rubiaceae)—that blossom more or less continuously, albeit at low density (Appanah 1979; Appanah and Chan 1981). One other section of mast-fruiting *Shorea* species (*Richetioides*), as well as the genus *Hopea*, appears to be pollinated wholly or in part by thrips and shares the same floral syndrome as *Shorea* section *Mutica* (see Appanah 1979). *Shorea* and *Hopea* are by far the larger genera of the Dipterocarpaceae (table 2) and play an exceptionally prominent role in mass-flowering events in aseasonal Malesia (Appanah 1979, 1981, 1985; Ashton 1982).

Planthoppers (Homoptera: Cicadellidae: *Varicopsella*) pollinate species of *Shorea* section *Shorea*, and bugs (Hemiptera: Miridae: *Decomia*) pollinate *Shorea* section *Brachypterae* (see Appanah 1987); both groups of insects share the fecun-

TABLE 2

NUMBERS OF SPECIES IN EACH DIPTEROCARP GENUS NATIVE TO MALESIA (BASED ON ASHTON 1982)

Genus	Malesian Species	Total Species	Genus	Malesian Species	Total Species
<i>Anisoptera</i>	10	11	<i>Neobalanocarpus</i>	1	1
<i>Cotylelobium</i>	3	5	<i>Parashorea</i>	10	14
<i>Dipterocarpus</i>	54	69	<i>Shorea</i>	163	194
<i>Dryobalanops</i>	7	7	<i>Upuna</i>	1	1
<i>Hopea</i>	84	102	<i>Vatica</i>	55	65

dity of thrips but apparently do not feed on dipterocarp corollas. Interestingly, members of neither section reach the abundance of those of *Shorea* section *Mutica* in Malesian forests, nor are they represented by comparable numbers of sympatric species.

Although several mass-flowering species of dipterocarps are pollinated by thrips, only two species (*Shorea multiflora* Barck (Syn.) and *Hopea pubescens* Ridl.) are known to be pollinated by the same species of thrips as are the six species of *Shorea* section *Mutica*. Both *S. multiflora* and *H. pubescens*, however, are rare and/or local in mixed lowland forest. In addition, no non-dipterocarp tree species engaging in mass flowering are known to be pollinated by any species of thrips. Thus, the species of *Shorea* section *Mutica* form a natural guild on which to focus analysis because they share pollinators that visit essentially no other species during mass-flowering events.

2. HOW DO DIPTEROCARP SPECIES AVOID COMPETITION FOR POLLINATION?

The flowering periods of the six species of *Shorea* section *Mutica* are staggered though strongly overlapping in time (fig. 2). In addition, the length of a species' flowering period tends to increase linearly with the mean date of its flowering, a point whose significance will be addressed presently. Staggering of flowering times is usually thought to result from selection to avoid hybridization, competition for pollinators, or clogging of stigmas by foreign pollen, by reducing overlap in flowering times (Levin and Anderson 1970; Mosquin 1971; Heithaus et al. 1975; Heinrich 1976; Stiles 1977, 1978, 1979; Waser 1978). Avoidance of hybridization appears unimportant in this case because all species show strong post-fertilization barriers to interspecific mating (Ashton 1982). Thus, to the extent that the observed flowering pattern reduces overlap in flowering times, it probably serves to reduce competition for the shared thrip pollinators and/or to avoid reduction of fecundity by clogging of stigmas with foreign pollen. How can we determine whether the observed flowering pattern differs from random and significantly reduces overlap?

The observed pattern involves species' flowering periods of 16 to 26 days, and a total flowering season from earliest to latest flowering of 76 days (Chan 1977, 1981). The total amount of interspecific floral overlap is 45 days. Four models can be advanced to test whether the observed flowering pattern significantly reduces overlap.

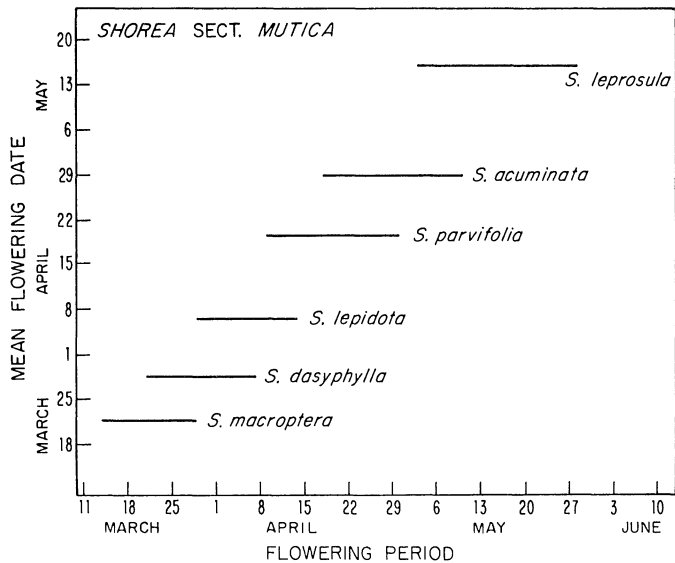


FIG. 2.—Staggering of flowering periods for species of *Shorea* section *Mutica* at Pasoh in 1976. Mean flowering dates represent the average of the earliest and latest dates of flowering for each species.

Model 1 (Cole test).—The most widely accepted model for testing the null hypothesis, introduced by Cole (1981) and modified by Fleming and Partridge (1984), randomly drops flowering periods of the observed lengths onto an interval of the same length as the actual flowering season. This process is iterated in a Monte Carlo simulation, and the distribution of the total days of interspecific overlap in flowering is compared with the actual overlap to determine the probability of obtaining the observed overlap by chance. For a given number of species and set of flowering-period lengths, total overlap is considered ecologically more meaningful than average pairwise overlap, because it measures interactions between a species and all potential competitors, and it is less distorted by low overlap values between a few pairs of species (Thomson and Rusterholz 1982).

In a simulation with 500 iterations, the mean overlap obtained for the six species of *Shorea* section *Mutica* was much greater than that observed (92.3 ± 28.7 days), and the observed flowering pattern significantly reduced overlap, resulting in a total overlap achieved by less than 0.4% of the randomly produced patterns. However, this model is flawed because dropping flowering periods at random onto the observed flowering season almost always results in a realized flowering season shorter than that actually observed (fig. 3). This occurs because the earliest flowering date realized in a given simulation is almost always later than the earliest possible flowering date, and the latest flowering date realized is almost always earlier than the latest possible date. Because a decrease in realized season length sharply increases the expected overlap (fig. 3), the Cole test is biased toward acceptance of significance. Whenever the potential flowering season is specified not by environmental conditions but, as is usually the case, by the time from

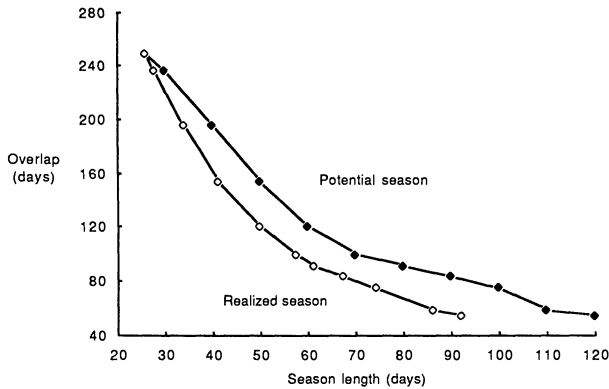


FIG. 3.—Average total period of interspecific overlap that results when flowering periods identical to those of species in *Shorea* section *Mutica* are dropped randomly onto a flowering season, as a function of season length. Overlap is plotted against the season length (“potential length”) assumed in the simulation (*solid symbols*), and against the mean realized length of time between earliest and latest flowering by members of the section (*open symbols*). The length of the realized season is considerably less than its potential length, and the amount of overlap increases nonlinearly as season length decreases.

observed earliest to latest flowering, the Cole test should be considered inappropriate.

Model 2 (Modified Cole test).—A simple modification of the Cole test would be to tune the potential flowering-season length so that the mean realized length equals the observed length. Simulations involving 100 iterations for potential seasons of 26–120 days revealed that a potential season of 100 days resulted in an actual season of roughly 76 days (fig. 3). In a simulation with 500 iterations for a 100-day potential season, the mean length of the actual season was 76.3 days and the mean overlap was 70.8 ± 27.0 days, which was not significantly more than the observed overlap of 45 days ($P > 14.6\%$). This test suggests the observed flowering pattern does not significantly reduce overlap, even though the observed overlap is only 1 day more than the theoretical minimum of 44 days! The problem is that, given fixed lengths of flowering periods, the expected amount of overlap drops as the length of the flowering season increases (fig. 3). As a result, simulation runs that result in a longer realized flowering season than observed have lower levels of overlap than would be expected if the actual (shorter) length of the flowering season had been used. Such spuriously low values tend to skew the lower tail of the distribution of all overlap values across all realized seasons so as to render many (otherwise exceptionally) low actual values of overlap statistically insignificant. This test is thus biased *against* acceptance of significance.

Model 3 (Null model).—One way to avoid these problems is to drop points randomly onto a unit interval, identifying each with the midpoint of a given flowering period, and then to expand the unit interval and associated flowering periods until they just cover the actual flowering season. In practice, this can be done by scaling the unit interval to the actual length of the flowering season, assuming that the earliest flowering of one species corresponds to the beginning of

the flowering season and that the latest flowering of another species corresponds to the end of the season. If x_i and x_j are the positions on the unit interval of the terminal species chosen, and m_i and m_j are the flowering-period lengths associated with these species, then the scaling factor s mapping $[0, 1]$ onto $[0, L]$ must satisfy

$$s(x_i - x_j) + 0.5(m_i + m_j) = L, \quad (1)$$

where $L = 76$ is the length of the actual flowering season. In this scaling, the points x_i and x_j are identified with $m_i/2$ and $L - m_j/2$, respectively. This results in the start of the flowering period of species i being identified with $m_i/2 - m_i/2 = 0$, and in the end of flowering by species j being identified with $(L - m_j/2) + m_j/2 = L$. Thus, the function mapping the unit interval onto the flowering season is

$$f(x) = s(x - x_i) + m_i/2. \quad (2)$$

This process is executed for all possible species pairs until a consistent scaling is achieved, in which (1) no species flowers before or after the assumed terminal species; (2) all species flower within the given flowering season and have flowering-period lengths equal to those observed; and (3) the realized length of the flowering season in the simulation equals the actual length assumed. A simulation of 500 iterations using this null model showed that the observed overlap in *Shorea* section *Mutica* is significantly lower than that expected at the 4.6% confidence level.

Model 4 (Null model with phylogenetic constraints).—A similar null model can be constructed incorporating phylogenetic constraints, based on the observed linear relationship between flowering period and mean flowering date. In this case, points are randomly dropped onto the unit interval, assigned appropriately scaled flowering periods based on their relative position in the flowering season, and then mapped onto the actual flowering season. One fact must be considered: the total length of the species' flowering periods in this model can range from roughly 102 to 146 days, compared with an actual total of 120 days, based on the relative position of the randomly placed points within the flowering season. A greater total length of flowering periods should lead, other things being equal, to greater total overlap. To compensate for this, we tabulated not total absolute overlap, but total overlap normalized by the total length of the flowering periods. A simulation of 500 iterations based on this normalized index showed that the observed overlap is significantly lower than expected at the 0.8% confidence level.

Degree of phenological overlap.—With the possible exception of Stiles' (1979) data on hummingbird-pollinated species in Costa Rica, which should now be reanalyzed using an approach similar to that of model 3, the flowering pattern shown by *Shorea* section *Mutica* seems to provide the only data that show a phenological overlap significantly lower than that of randomly generated flowering patterns (see Fleming and Partridge 1984; Kjellson 1985). Statistical significance was barely achieved in the *Shorea* case, even though the total overlap observed was only 1 day more than the theoretical minimum, suggesting that demonstrations of a significant reduction in phenological overlap may generally require flowering data from several years for a given suite of species. Even though a single

occurrence of a low-probability event may not be statistically significant, its constant recurrence would be.

Although the observed flowering pattern significantly reduces overlap toward the minimum consistent with the observed lengths of flowering periods and overall flowering season, the absolute amount of overlap is rather high (fig. 2). This may reflect the unusual degree of mutualism among competitors for a pollinator whose density can increase dramatically during—and as a result of—flowering by a single tree species. (Waser and Real [1979] presented evidence of mutualism in sequentially flowering plants visited by bees and hummingbirds, but that effect seems a more likely result of migration than of reproduction by those long-lived pollinators.) The negative selective impact of increased overlap with a preceding *Shorea* species can thus be partly outweighed by the benefits of the resulting increase in thrip density. Finally, in *Shorea* section *Mutica*, the inverse relationship between rates of fruit maturation and floral morphogenesis is a necessary prerequisite for the observed synchrony in fruiting and avoidance of competition for pollinators, and it provides additional support for the hypothesis that synchronous fruiting is selectively favored.

3. WHAT IS THE ENVIRONMENTAL CUE THAT TRIGGERS MASS FLOWERING?

Previous attempts to discover the environmental cue that triggers mass flowering have been stymied largely because there was no clear idea of how long before flowering the cue might occur. In most dipterocarp species, inflorescences are both axillary and terminal and replace one of the two leaf flushes that occur in each nonflowering year in aseasonal Malesia (Ashton, in press). In peninsular Malaysia, these flushes usually occur during the first and second period of somewhat drier conditions, in about January and July, when mean monthly precipitation reaches its two annual minima but does not fall below 100 mm; these periods correspond roughly to the ends of the early and late monsoon season in the Indian Ocean. The cue that ultimately triggers floral induction must precede the expansion of these inflorescence-bearing axes, which usually takes at least 1 mo (Chan and Appanah 1980), but how much earlier the cue itself occurs is not obvious.

The flowering pattern in *Shorea* section *Mutica* suggests a solution to this problem. As noted previously, there is a highly significant, linear increase in the length of a species' flowering period y with mean date of flowering x (1 = January 1, 1976):

$$y = 0.201x - 1.385 \quad (3)$$

(fig. 4; principal-axis regression, $r = 0.979$, $df = 4$, $P < 0.001$; Sokal and Rohlf 1981). Using this relationship, we can extrapolate back to the mean flowering date that would result in a flowering period of zero length. We infer that this is the date of floral induction, on the basis of the following argument.

Flowering within each species appears controlled by an endogenous rhythm triggered by an external cue, based on (1) the near-synchrony and regular sequence of flowering, (2) the interspecific synchrony in fruiting, (3) the apparent repetition of the observed species flowering sequence in *Shorea* section *Mutica*

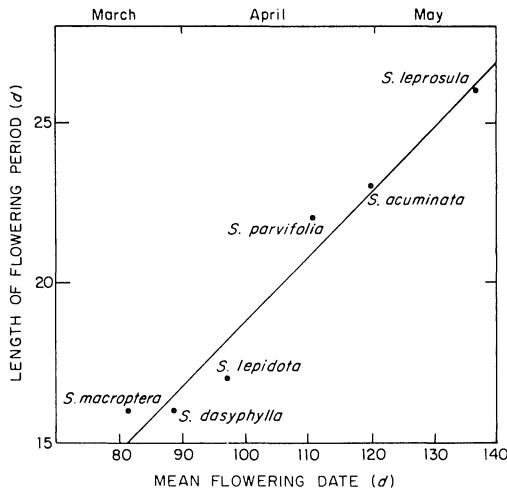


FIG. 4.—Length of species' flowering periods as a function of mean flowering date in *Shorea* section *Mutica* (eq. 3).

during at least two other mass-flowering events (table 3), (4) the temporally aperiodic but regionally coherent pattern of occurrence of mass-flowering events, and (5) the participation of non-dipterocarps (e.g., Burseraceae, Fabaceae, Polygalaceae, Sapotaceae) in these mass flowerings.

Thus, a population of trees (or physiologically somewhat independent branches) can be considered analogous to a boxful of (slightly inaccurate) alarm clocks. If the clocks are all synchronized and set at a given time, the length of time over which the box will ring—or the population flower—will increase linearly with the mean alarm or flowering time and be zero at the time of clock setting or floral induction. According to this argument, the expected date of floral induction is January 11, with a 95% confidence interval of ± 29.5 days (fig. 5). The floral cue thus appears to occur roughly 9 wk before flowering by *S. macroptera*, the first

TABLE 3

NUMBERS OF INDIVIDUALS OF SPECIES IN *SHOREA* SECTION *MUTICA* BLOSSOMING IN DIFFERENT MONTHS DURING MASS-FLOWERING EVENTS IN 1980 AND 1984

SPECIES	1980					1984			
	Mar	Apr	May	June	Mean Date*	Aug	Sep	Oct	Mean Date*
<i>S. macroptera</i>	10	1			3.09	19			8.00
<i>S. dasyphylla</i>						3	3		8.50
<i>S. lepidota</i>						6	4		8.40
<i>S. parvifolia</i>		49	51	2	4.54	33	34	10	8.70
<i>S. acuminata</i>		15	19		4.56	16	10	11	8.86
<i>S. leprosula</i>		17	25		4.60	25	24	24	8.99

NOTE.—For mean date, January = 1.

* SOURCE.—Forest Department records, Kepong.

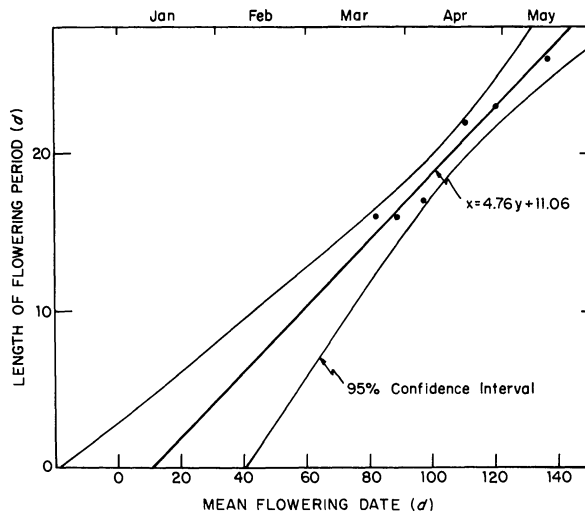


FIG. 5.—Extrapolation of regression line relating mean flowering date to flowering-period length in *Shorea* section *Mutica*, to obtain an estimate of time of floral induction on January 11 (see the text). To obtain confidence limits for the mean flowering date corresponding to a flowering period of zero length, we conducted a least-mean-squares regression (Sokal and Rohlf 1981) of mean flowering date on flowering-period length. The x -intercept of the principal-axis regression is January 7, quite close to that obtained using the least-mean-squares regression.

species in the flowering sequence, and roughly 16.5 wk before flowering by *S. leprosula*, the last species in the sequence.

Potential Environmental Cues

Several environmental events have been proposed as floral triggers for mass flowering in dipterocarps, including prolonged drought (Foxworthy 1932; Boswell 1940; Wood 1956; Baillie 1972; Burgess 1972; Medway 1972; Janzen 1974; Whitmore 1984; Appanah 1985), increased number of cloudless hours of direct sunlight (Wycherley 1973; Ng 1977), and a drop or rise in mean temperature (Wycherley 1973; Appanah 1985). In addition, canopy position and plant nutritional status have been implicated as secondary factors modulating reproduction by individual trees (Burgess 1972; Fox 1972).

Light plays some role in floral induction, because canopy dipterocarp species flower only after their crowns emerge into direct sunlight; non-emergent species can flower before they reach their maximum height (Fox 1972). However, by itself, photoperiod (well established as a flower-inducing signal in many plant species; e.g., Audus 1972; Wycherley 1973; Vince Prue et al. 1984) seems unlikely to trigger flowering in dipterocarps: mass dipterocarp flowering in peninsular Malaysia starts in February or March, whereas flowering usually starts in July in northwestern Borneo at the same latitude (Ashton, in press). Furthermore, although mass flowerings in peninsular Malaysia are most likely to occur from

March through May, such events occasionally occur from October through December (e.g., see table 3).

If photoperiod is invoked to explain the first of these cases, then we must assume that populations of several dipterocarp species must respond, in concert, to different photoperiods on different islands: five of the six species of *Shorea* section *Mutica* participating in mass flowering in peninsular Malaysia participate in mass flowering in Borneo. If photoperiod is invoked to explain the second case, then the seasonal variation in day length, the initial dates of mass flowering in March or October, and the (reasonable if unsupported) assumption that each *Shorea* species responds to only one critical day length imply that the photoperiodic cue would have to occur some multiple of 6 mo before flowering. This seems far too early given the predicted date of floral induction only 63 ± 30 days before flowering.

Tree nutritional status probably also plays some role in floral induction. In any mass flowering, not all individuals of a given species produce blossoms. For example, by monitoring tagged trees, Burgess (1972) found that when heavy-fruited years came in close succession in *S. curtisii* and *S. platyclados*, only one of the individuals that flowered in 1968 did so again in 1970. Nevertheless, it seems unlikely that the nutritional status of individual trees constrains mass flowering at the population level, given that many individuals in each species do not flower in any given event; presumably, several successive events would be required before nutritional inhibition became population- or community-wide.

Drought is broadly correlated with mass flowering in peninsular Malaysia and Borneo (Wood 1956; Burgess 1972; Medway 1972; Cockburn 1975). However, Wycherley (1973) pointed out that, although in peninsular Malaysia somewhat drier conditions occur during two annual periods that do not differ substantially in rainfall, flowering seasons recorded up to 1973 were known only to follow the onset of the first. Further, even though flowering can occur at different times at different altitudes and on different soils—which often support different suites of species (Wood 1956; Sasaki et al. 1979; Ashton 1982)—there is no close correlation between flowering intensity and local physiography and, thus, water availability (Chan 1977, 1981). Thus, drought per se (namely, water shortage) is unlikely to be the floral trigger because mass flowering is regional and apparently unaffected by the differential distribution of individual trees relative to the water table. The floral trigger, whatever it is, must be regional in nature and occur at multi-year intervals.

In this connection, it is interesting that the mean timing of relatively dry periods and the usual time of mass flowering in *Shorea* are not clearly associated in aseasonal Malesia (fig. 6). Rainfall seasonality, as judged by variation in monthly mean precipitation, varies on a local scale. For example, in Sumatra and western Borneo, nearby stations receive their lowest rainfall in either the first or second half of the year, but there does not appear to be any corresponding differentiation in the season of mass flowering. Furthermore, stations in eastern peninsular Malaysia and southwestern Borneo achieve their lowest mean monthly rainfall in January, but most mass flowerings in eastern peninsular Malaysia occur from

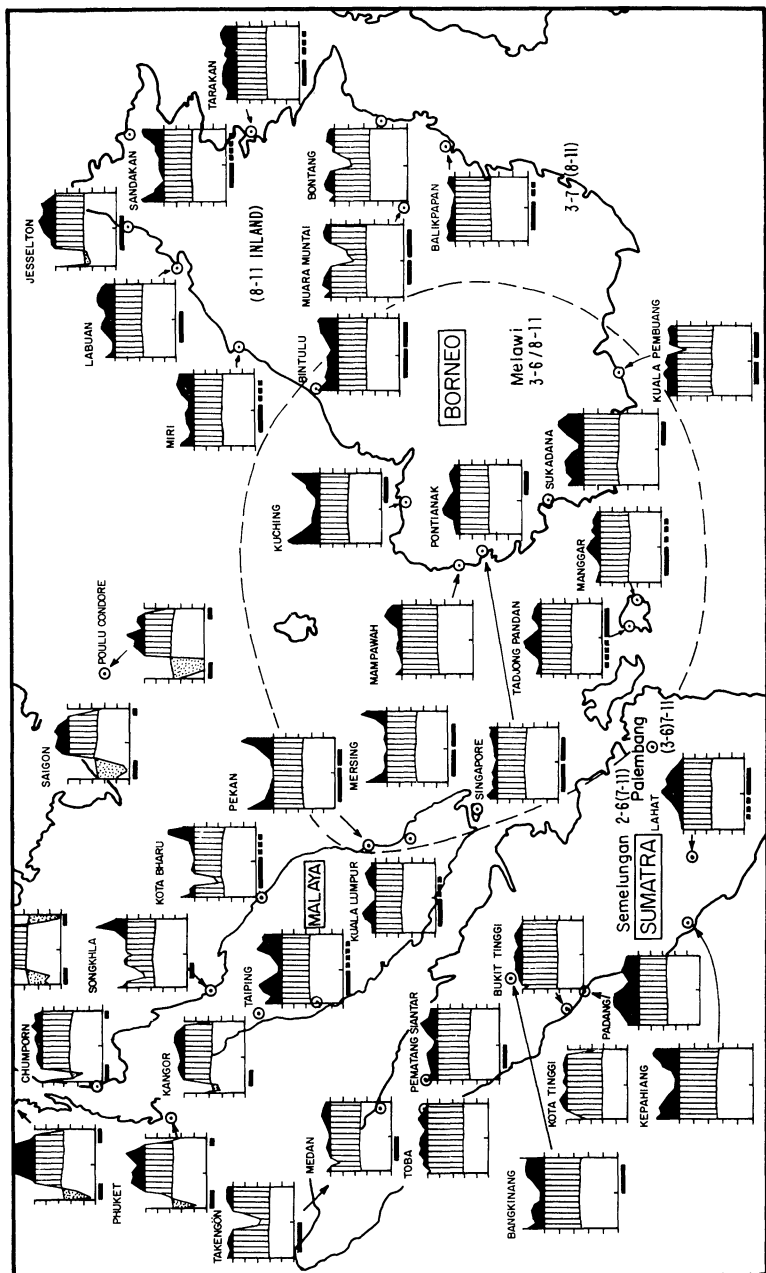


FIG. 6.—Regional patterns of mean monthly rainfall (*upper line*) and temperature (*lower line*), and predominant months of dipterocarp flowering in western Malesia excluding the Philippines. Scales indicate rainfall (2-cm intervals) or temperature (10°C intervals); monthly rainfall in excess of 10 cm is considered to exceed monthly evapotranspiration. Sources: Walter and Lieth 1967; Kuswata, unpubl. data. For the widespread early-flowering *Shorea macroptera* ($N = 88$) and *S. multiflora* ($N = 70$), the mid-season-flowering *S. parvifolia* ($N = 162$), and the late-flowering *S. leprosa* ($N = 108$), flowering months were derived from specimens in the Harvard University Herbaria as indicated by bars below the graphs, or by month number if meteorological data were unavailable. On the evidence of specimen-label data, individuals can flower in the first or second half of the year throughout the region; the bars therefore identify only the principal months of flowering. Dashed bars (or parenthetical month numbers) indicate a significant but subordinate flowering frequency.

February to July, whereas those in western Borneo occur from August through November (fig. 6).

Ng (1977) showed that the months with the highest average sunshine records (February and March) nearly coincide with the onset of mass flowerings in peninsular Malaysia. Before 1981, however, mass flowering had never been recorded in any other month, even though any month between January and August can receive the most sunshine in any particular year (see Wycherley 1973). Ng (1977) asserted that mass flowerings early in the year were consistently associated with unusually high increases in sunshine, an average of at least 2 h, per day over the preceding month.

Wycherley (1973) suggested that unusual temperature conditions—in terms of mean maximum temperature, mean minimum, or mean daily range—may be responsible for floral induction in dipterocarps, and he presented correlations between such indexes and mass flowering. However, his analysis, together with all other studies that attempt to relate mass flowering to drought, temperature, or cloudlessness, is suspect because it relied on crude monthly or yearly statistics that are likely to swamp any sharply defined but short-lived triggering event. Detailed analysis of weekly meteorological records (Appanah, MS) has shown no unflinching association of mass flowerings with the length of rainless periods, mean temperatures, or sunlit cloudless hours. Long droughts often precede mass flowerings, but droughts of similar length often fail to elicit a flowering event.

Analysis of Daily Meteorological Data

Daily thermal maxima—or, by inference, daily thermal range—seem unlikely as floral cues given the high short-term temporal and spatial variation expected in these measures on the basis of variations in cloudiness, crown position, transpiration rate, and root position relative to the water table.

Nighttime minimum temperature, however, might be a useful cue. In the aseasonal wet tropics it should be constrained by high relative humidity to a relatively high and narrow temperature range. Indeed, at Pasoh during several months preceding the suspected time of floral induction, minimum nighttime temperatures occupied a rather narrow range of 21.0° to 23.5° C; during mid to late January, these temperatures dropped frequently below 20.5° C to as low as 18.9° C for several days at a time. To test whether this small, short-term drop in nighttime temperature was consistently associated with mass flowering, we examined the long-term meteorological records available for the Kepong Arboretum in peninsular Malaysia, where flowering events in *Shorea* section *Mutica* occurred in March 1976, late August 1981, March 1982, and late August 1985. Figure 7 presents the 4-day running means of maximum and minimum daily temperatures at Kepong from 1975 to 1985. The occurrence of mass flowering in the latter half of 1981 and 1985 were the first such events during the second “dry” season recorded for peninsular Malaysia and provided special impetus for checking whether the proposed temperature cue was associated with these events as well.

As can be seen, a drop in minimum nighttime temperatures of at least 5 to 8 days was associated with each flowering event and preceded it by the expected 8 to 9 wk. No such consistent drop occurred outside an association with a flowering

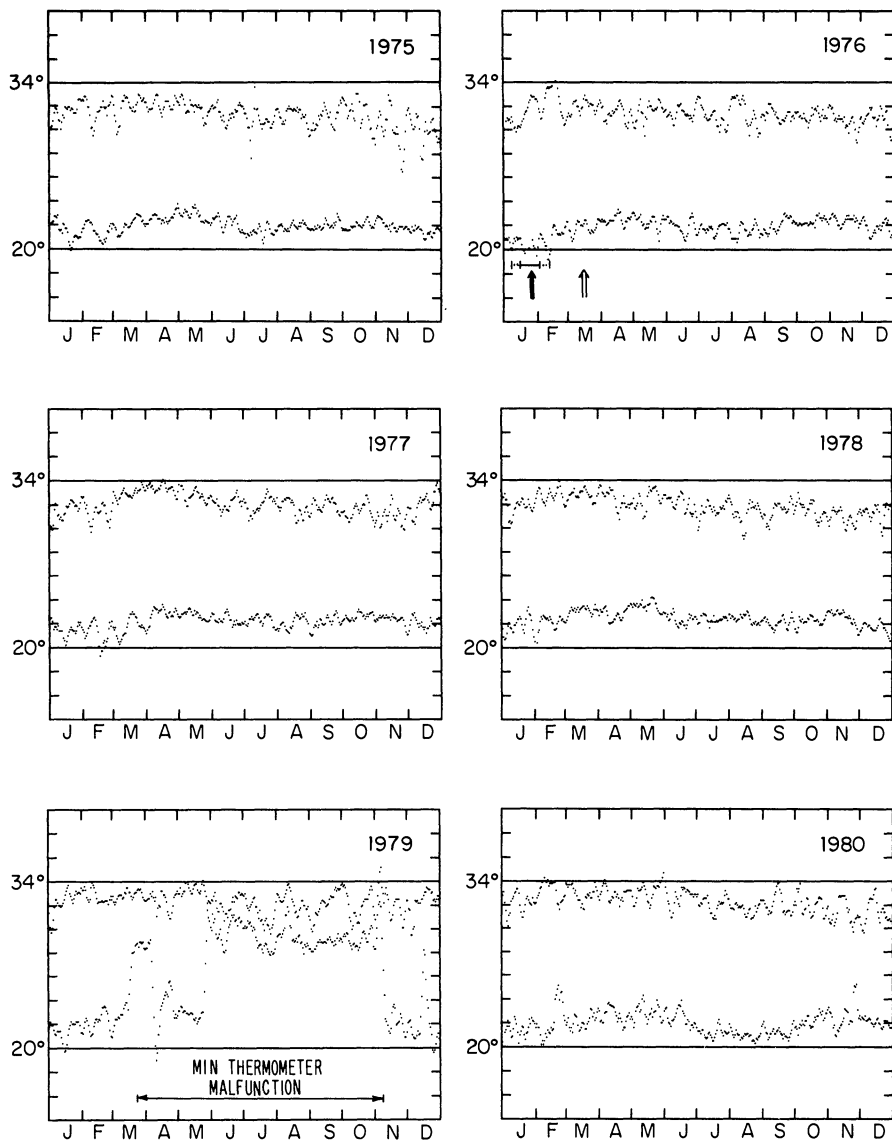
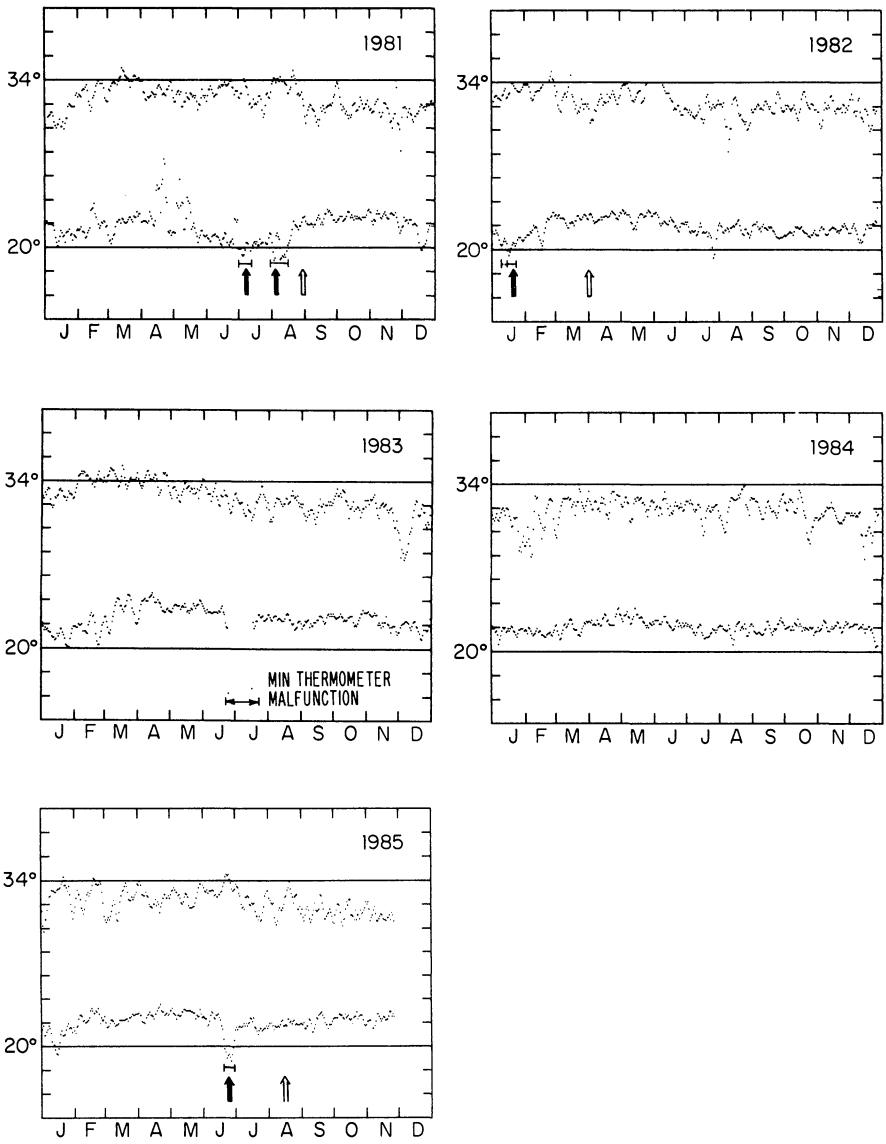


FIG. 7 (above and on facing page).—Maximum and minimum daily temperatures at Kepong, 1975–1985 (Forest Department records); 4-day running means are plotted. *Solid arrows*, Prolonged drops in the running mean minimum temperature below 20° C (20.2° C in 1982); in each instance, these correspond to a mass-flowering event that occurred roughly 2 mo later (*open arrows*). Conversely, no mass-flowering events during 1975–1981 occurred near Kepong in the absence of such a drop. (The minimum thermometer malfunctioned for several months in 1979 and in June–July 1983, preventing the recording of useful data during these periods.)



event, and this drop preceded the unusual late-season *Shorea* flowerings in 1981 and 1985, as well as the early-season flowerings in 1976 and 1982. Often slightly lagging the drop in minimum temperature is an increase in maximum temperature and daily temperature range, both of which show, however, considerably more variation than minimum temperature alone.

We infer that the drop in minimum nighttime temperature and increase in daily temperature range result from the occasional penetration of dry air masses into the aseasonal Malesian tropics. The drop in minimum temperature is, we believe, the best proximal cue for this invasion. Drops in humidity and rainfall can be obscured by differences in site drainage and exposure; rainfall and cloudiness can decrease without a substantial drop in bulk atmospheric humidity; and maximum temperature shows considerable temporal and spatial variability. It is remarkable that a drop of only 2°C in minimum temperature for several nights might be sufficient to elicit flowering. This proposed cue should now be directly tested by manipulating the thermal environment to which dipterocarps are exposed.

It must be emphasized that the blossoming of certain tropical orchids (e.g., *Dendrobium crumenatum*, *Bromheadia finlaysoniana*, *Epiphyllum oxypetalum*) a few days after a short, steep drop in temperature associated with thunderstorms (Coster 1925, 1926; Holttum 1949, 1954) is not at all comparable to the thermal response envisioned for dipterocarps because it involves the simple release of previously developed buds, not the initiation of development of floral primordia.

4. WHAT FACTORS LED TO A PHENOLOGICAL CORE FAVORING THE EVOLUTION OF GENERAL MAST FRUITING?

In seasonal tropical areas of southeastern Asia and India, dipterocarps apparently use the same cue of a drought-associated temperature drop to initiate floral development. Dipterocarps in these areas flower annually during the single dry season and fruit at the beginning of the rainy season (Ashton 1982, in press). Use of the drought-associated temperature drop thus has an immediate ecological advantage in terms of pollination and seedling ecology, whereas its only immediately apparent advantage for species in the aseasonal tropics is the synchronization of interspecific flowering, which presumably could be achieved using another cue. This suggests that dipterocarps, a dominant group in aseasonal tropical rain forests, may have initially evolved in the seasonal tropics. This same conclusion has been reached independently using taxonomic and biogeographic evidence (Ashton 1982).

Mast fruiting in the aseasonal tropics may thus have evolved largely as a result of developmental constraints in a group that arose in the seasonal tropics. As a result of the shared temperature cue, and in the absence of an overriding endogenous rhythm, several species of dipterocarps in an area would come into flower and fruit more or less synchronously at irregular, multi-year intervals when a dry air mass penetrated that portion of the aseasonal tropics. This would form a phenological core of species. Selection based on this core could entrain and synchronize species in several other families to form the observed phenomenon of

general mast fruiting. For the most numerous of these tree species, thrips may provide one of the few viable means of animal-mediated cross-pollination at irregular intervals of several years. Less common species can rely on longer-lived, less fecund pollinators that are maintained at low density between mass flowerings by scattered understory flowers. Indeed, Appanah (1979, 1981) found that many less common mass-flowering tree species in genera such as *Xanthophyllum* (Polygalaceae), *Sindora* and *Millettia* (Fabaceae), and *Mesua* (Clusiaceae) are pollinated principally by *Xylocopa* bees. Interestingly, dipterocarps that flower almost every year in aseasonal Malesia (e.g., *Neobalanocarpus heimii*, *Dryobalanops aromatica*, *D. oblongifolia*, some *Dipterocarpus*) are unusual in being highly gregarious and are pollinated by *Apis* and *Trigona* bees (Appanah 1987). Bee pollination is said to be the rule among the annually flowering dipterocarps of seasonal Asia (Ashton, in press).

The scenario we have proposed for the origin of mast fruiting differs from those advanced by Janzen (1974), who proposed either the origin of mast fruiting in one dipterocarp species of many already present in a habitat, leading to entrainment of other species, or the (more likely) origin in a species completely dominating a habitat, leading to entrainment of other species as they invade. Although our scenario and Janzen's agree in assuming that predator satiation in unproductive habitats was the principal factor that ultimately led to the evolution of mass fruiting, they differ in the mechanism by which an original "phenological core" of mast-fruiting species arose.

POTENTIAL RELATIONSHIP OF FLORAL CUE TO GLOBAL CLIMATIC PATTERNS

Finally, one might ask what triggers the invasion of a dry air mass into the aseasonal tropics and provokes a mass flowering. In many areas, particularly the western sides of the Malaysian peninsula, Borneo, and Sumatra, a chance fluctuation in the subtropical monsoonal circulation system appears most likely. Indeed, in this regard as in so many other aspects of tropical plant biology, the native peoples of the Malesian rain forests may have anticipated our conclusion. It is a well-known saying among the Malays that "The dry monsoon is the mother of the dipterocarps."

On the eastern sides of the Malesian landmasses, however, we believe that the El Niño–Southern Oscillation phenomenon may have an important role. The shifting of currents and warming of the ocean surface off Peru have important effects on the climate in the western Pacific (Barber and Chavez 1983; Cane 1983; Rasmussen and Wallace 1983; Rasmussen 1985). The most important effect is that, early in the El Niño cycle, the warm surface temperature of the eastern Pacific causes greater atmospheric convection there and induces an anomalous easterly flow of air from the western Pacific. This tends to cut the trade winds that are a major source of orographic rainfall on the eastern slopes of Borneo, Sumatra, and the Malaysian peninsula. Leighton and Wirawan (1986) have indeed shown an exact correspondence between El Niño events and droughts in eastern Borneo over the past 45 years. It is possible that El Niño–induced droughts trigger

TABLE 4
 TEMPORAL RELATIONSHIP BETWEEN EL NIÑO YEARS AND STRONG OR SOMEWHAT WEAKER
 MAST-FRUITING EVENTS IN WESTERN (LEEWARD) AND EASTERN (WINDWARD)
 PORTIONS OF PENINSULAR MALAYSIA AND BORNEO

EL NIÑO YEARS	MAST-FRUITING EVENTS			
	West Peninsular Malaysia	East Peninsular Malaysia	West Borneo	East Borneo
50				
51		•		•
52				•
53		•	•	
54				•
55	•	•		•
56				
57	•	•	•	
58	•		•	•
59				•
60		•		•
61			•	
62				
63	•	•		•
64				
65			•	
66				
67			•	•
68	•	•		•
69			•	
70				
71				
72			•	•
73				•
74				
75				
76	•	•	•	•
77				•
78				
79			•	
80			•	
81	•		•	•
82		•	•	
83	•			•

NOTE.—El Niño years are in boldface. Large dots represent strong mast-fruiting events; small dots, somewhat weaker events.

SOURCE.—Data on El Niño–Southern Oscillation events: Rasmussen and Wallace 1983; Rasmussen 1985. Data on mast-fruiting events: reports of state forest departments, supplied monthly to the Forest Research Institute (peninsular Malaysia); annual publication of illipe-nut exports in the Annual Reports of the Sarawak Forest Department up to 1965, and thereafter in the Sarawak *Gazette* (western Borneo); and Annual Reports of the Sabah Forest Department (eastern Borneo).

mass flowering in dipterocarps growing in these regions. Certainly the last two major El Niño events, in 1976–1977 and 1982–1983, have been accompanied by heavy mass flowering in many areas throughout Malesia.

To test this idea, we examined the relationship between El Niño–Southern Oscillation events and mass flowering in four regions: eastern peninsular Malaysia and eastern Borneo (Sandakan), and western peninsular Malaysia (Selangor) and western Borneo (Kuching) (table 4). In three cases, the biological data are based on mass flowerings recorded by the forest departments; the data from western Borneo are the yearly reports on the export of illipe nuts (fruit of *Shorea* section *Pachycarpae*). Illipe nuts are an important commercial item gathered in the year following mass-flowering years. The illipe-nut data have thus been adjusted so as to make them comparable to the data on mass flowering. An attempt was made to distinguish relatively strong and weak flowering events using the available records. Reliable data, unaffected by the vicissitudes of World War II and the ensuing Communist insurgency in Malaysia, are available for the period from 1950 to 1983.

According to negative values of the Southern Oscillation index, which is strongly correlated with sea-surface-temperature anomalies in the eastern Pacific, El Niño years occurred in 1950–1951, 1953–1954, 1957–1958, 1965–1966, 1968–1969, 1971–1972, 1976–1977, and 1982–1983, with an additional weak event in 1963 (fig. 7). Using the total number of mass-flowering events for a given region, we conducted Monte Carlo simulations to determine whether a significantly greater number of coincidences than expected arose between El Niño events and mass-flowering years. In eastern peninsular Malaysia, seven of nine flowering events ($P < 0.058$), and all six strong flowering events ($P < 0.016$), coincided with El Niño years, confirming the expected trend on windward portions of Malesian landmasses. In western peninsular Malaysia and western Borneo, mass flowering is not significantly related to El Niño events, as expected. Finally, in eastern Borneo there is also no significant relationship, belying the expected positive association. However, the Sandakan flowering data are suspect for two reasons. First, the Forest Department there may have lumped records for all of northern Borneo, including sites on either side of the central mountain range. Wood (1956) stated that flowering events tend to occur in different seasons on the different sides of the range. Second, sites in this northeasterly region are near the terminus of the central mountain range, and thus at the periphery of any orographic influence that it may exert; note that the climate diagrams from Sandakan and Labuan on opposite sides of northern Borneo are qualitatively quite similar but different from those representing sites farther south in eastern Borneo. Unfortunately, reliable flowering data are not available from these sites farther south.

Nevertheless, from the reliable data available from eastern peninsular Malaysia, mass flowering and El Niño–Southern Oscillation events appear strongly related. Furthermore, preliminary reports from peninsular Malaysia (J. LaFrankie, pers. comm.) and Borneo (L. Curran, pers. comm.) as this paper goes to press confirm the expected occurrence of a mass flowering starting in March 1987 following a mild El Niño event this past winter. It would indeed be surprising if the two most noteworthy, aperiodic multi-year phenomena in the tropics—the an-

chovy decline and the consequent guano bird die-off in the eastern Pacific, and mast fruiting of dipterocarps in the Malesian tropics—were in some cases connected by a common underlying cycle of the ocean and atmosphere.

SUMMARY

The supra-annual mast fruiting of dipterocarps, dominant trees of Far Eastern lowland rain forests, has been considered an adaptation to reduce seed predation through satiation. However, this explanation raises four important questions. (1) What pollinates species that flower at intervals of more than one year? (2) How do mass-flowering species avoid competition for pollinators? (3) What is the environmental cue for floral induction that induces scores of species in several families to flower at irregular intervals of more than one year in an aseasonal climate? (4) And, most important, what factors could cause an initial phenological aggregation of species' fruiting times? Once such a phenological core of species exists, selection for predator satiation could entrain other species into the same fruiting schedule and perfect the synchrony of seed release. The essential question is how such a phenological core of species, flowering at irregular intervals in an aseasonal climate, could initially arise.

The observations and analyses presented here indicate that the answers to these questions are intricately related to each other and to the El Niño–Southern Oscillation phenomenon. (1) Several mass-flowering dipterocarps are pollinated by thrips, which persist at low levels between mass flowerings and can explode in density as the dipterocarps come into flower. (2) Mass-flowering dipterocarp species in *Shorea* section *Mutica* significantly reduce the overlap in flowering times by staggering their flowering periods, thereby reducing competition for pollinators and/or the clogging of stigmas with foreign pollen. The new technique used to analyze whether a particular pattern of resource use significantly reduces overlap overcomes an error inherent in previous techniques, and it should be used whenever the total flowering season or range of resources is determined not by external conditions, but by the range of flowering times or resources used by the species in question. (3) The time of floral induction in *Shorea* section *Mutica* is derived using the linear relationship between the duration of each species' flowering period and mean flowering date. An analysis of meteorological records suggests that induction is caused by a drop of roughly 2°C or more in minimum nighttime temperature for three or more nights. This extraordinary trigger is probably the most reliable signal associated with an invasion of the aseasonal tropics by a dry air mass. (4) Such a trigger does not appear to be directly adaptive in the aseasonal tropics, but in the seasonal tropics it would result in flowering at the onset of dry season and ripening fruits at the beginning of rainy season. This suggests that the Dipterocarpaceae may have arisen initially in the seasonal tropics, even though their center of species diversity is now in the aseasonal tropics. Invasion of the aseasonal tropics by trees having such a floral trigger, adapted to the seasonal tropics, could help explain the origin of a phenological core of species flowering and fruiting more or less synchronously at intervals of several years. The droughts causing these mass flowerings may, in some cases, be

driven by the climatic effects of the El Niño–Southern Oscillation phenomenon in the western Pacific, as evidenced by the temporal association of El Niño years with drought and mast fruiting on windward slopes of tropical Malesia.

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LITERATURE CITED

- Appanah, S. 1979. The ecology of insect pollination of some tropical rain forest trees. Ph.D. diss. University of Malaya, Kuala Lumpur, Malaysia.
- . 1981. Pollination in Malaysian primary forests. *Malay. For.* 44:37–42.
- . 1985. General flowering in the climax rain forests of Southeast Asia. *J. Trop. Ecol.* 1:225–240.
- . 1987. Insect pollination and the diversity of dipterocarps. Pages 277–291 in A. J. G. H. Kosterman, ed. *Proceedings of the Third Roundtable Conference on Dipterocarps*. UNESCO, Jakarta, Java.
- Appanah, S., and H. T. Chan. 1981. Thrips: the pollinators of some dipterocarps. *Malay. For.* 44:234–252.
- Ashton, P. S. 1964. *Ecological studies in the mixed dipterocarp forests of Brunei State*. Oxford For. Mem. 25. Clarendon, Oxford.
- . 1982. Dipterocarpaceae. *Flora Malesiana ser. 1, Spermatophyta* 9:251–552.
- . In press. Dipterocarp reproductive biology. In H. Lieth and M. J. A. Werger, eds. *Ecosystems of the world*. Vol. 14B. *Tropical rain forest ecosystems: biogeographical and ecological studies*. Elsevier, Amsterdam.
- Audus, L. J. 1972. *Plant growth substances*. Barnes and Noble, New York.
- Baillie, I. C. 1972. Further studies on the occurrence of drought in Sarawak. Soil Survey Report F7. Forest Department, Kuching, Malaysia.
- Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. *Science (Wash., D.C.)* 222:1203–1210.
- Becker, P. 1983. Effects of insect herbivory and artificial defoliation on survival of *Shorea* seedlings. Pages 241–252 in S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, eds. *Tropical rain forests: ecology and management*. Blackwell, Oxford.
- Boswell, A. B. S. 1940. Rainfall and the flowering of *Shorea*. *Malay. For.* 9:175–177.
- Burgess, P. F. 1972. Studies on the regeneration of the hill forests of the Malay peninsula: the phenology of dipterocarps. *Malay. For.* 35:103–123.
- Cane, M. A. 1983. Oceanographic events during El Niño. *Science (Wash., D.C.)* 222:1189–1194.
- Chan, H. T. 1977. *Reproductive biology of some Malaysian dipterocarps*. Ph.D. diss. University of Aberdeen, Aberdeen, Scotland.
- . 1981. Reproductive biology of some Malaysian dipterocarps. III. Breeding systems. *Malay. For.* 44:28–36.
- Chan, H. T., and S. Appanah. 1980. Reproductive biology of some Malaysian dipterocarps. I. Flowering biology. *Malay. For.* 43:132–143.
- Cockburn, P. S. 1975. Phenology of dipterocarps in Sabah. *Malay. For.* 38:160–170.
- Cole, B. J. 1981. Overlap, regularity, and flowering phenologies. *Am. Nat.* 117:993–997.
- Coster, C. 1925. Eendagsorchideen. *Trop. Nat.* 14:121–126.
- . 1926. Periodische Blüteerscheinungen in den Tropen. *Ann. Jard. Bot. Buitenzorg* 35:125–162.

- Daljeet Singh, K. 1975. A preliminary survey of insect attack on seedlings and saplings in Bukit Belata Forest Reserve. *Malay. For.* 38:14–16.
- Fleming, T. H., and B. L. Partridge. 1984. On the analysis of phenological overlap. *Oecologia (Berl.)* 62:344–350.
- Fox, J. E. D. 1972. The natural vegetation of Sabah and natural regeneration of the dipterocarp forests. Ph.D. diss. University of Wales, Bangor.
- Foxworthy, F. W. 1932. Dipterocarpaceae of the Malay peninsula. *Malay. For. Rec.* 10.
- Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. *Ecology* 57:890–899.
- Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Patterns of foraging and resource utilization in several species of bats in a seasonal tropical community. *Ecology* 56:841–854.
- Holtum, R. E. 1949. Gregarious flowering of the terrestrial orchid *Bromheadia finlaysoniana*. *Garden's Bull. (Singapore)* 12:295–302.
- . 1954. *Plant life in Malaya*. Longmans, Green, London.
- Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 4:69–103.
- Kjellson, G. 1985. Seed fall and phenological overlap in a guild of ant-dispersed herbs. *Oecologia (Berl.)* 68:140–146.
- Leighton, M., and N. Wirawan. 1986. Catastrophic drought and fire in Borneo rain forests associated with the 1982–83 El Niño Southern Oscillation event. Pages 83–107 in G. T. Prance, ed. *Tropical rain forests and the world atmosphere*. Westview, Boulder, Colo.
- Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *Am. Nat.* 104:455–467.
- McClure, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malay. For.* 29:182–203.
- Medway, Lord. 1972. Phenology of a tropical rain forest in Malaya. *Biol. J. Linn. Soc.* 4:117–146.
- Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22:398–402.
- Ng, F. S. P. 1977. Gregarious flowering of dipterocarps in Kepong, 1976. *Malay. For.* 40:126–137.
- Rasmussen, E. M. 1985. El Niño and variations in climate. *Am. Sci.* 73:168–177.
- Rasmussen, E. M., and J. M. Wallace. 1983. Meteorological aspects of the El Niño/Southern Oscillation. *Science (Wash., D.C.)* 222:1195–1202.
- Ridley, H. N. 1901. The timbers of the Malay peninsula (cont'd). *Agricultural Bulletin of the Straits and Federated Malay States* 1. Government Printing Office, Singapore.
- Sasaki, S., C. H. Tan, and A. R. Zulfatah. 1979. Some observations of unusual flowering and fruiting of dipterocarps. *Malay. For.* 42:38–65.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Freeman, San Francisco.
- Stiles, F. G. 1977. Coadapted pollinators: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science (Wash., D.C.)* 198:1177–1178.
- . 1978. Temporal organization of flowering among the hummingbird foodplants of a tropical wet forest. *Biotropica* 10:194–210.
- . 1979. Reply to Poole and Rathcke. *Science (Wash., D.C.)* 203:471.
- Thomson, J. D., and K. A. Rusterholz. 1982. Overlap summary indices in the detection of community structure. *Ecology* 63:274–277.
- Vince Prue, D., B. Thomas, and K. E. Kockshull. 1984. *Light and the flowering process*. Academic Press, New York.
- Walter, H., and H. Lieth. 1967. *Klimadiagramm-Weltatlas*. Fischer, Jena, West Germany.
- Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934–944.
- Waser, N. M., and L. A. Real. 1979. Effective mutualism between sequentially flowering plant species. *Nature (Lond.)* 281:670–672.
- Whitmore, T. C. 1984. *Tropical rain forests of the Far East*. 2d ed. Oxford University Press, Oxford.
- Wood, G. H. S. 1956. The dipterocarp flowering season in North Borneo, 1955. *Malay. For.* 19:193–201.
- Wycherley, P. R. 1973. The phenology of plants in the humid tropics. *Micronesica* 9:75–96.