The Phenology of Plants in the Humid Tropics

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Abstract

Meteorological phenomena (as indicated by cloudiness and hours of bright sunshine) reinforce or modify the relatively small differences in daylength which result from astronomical conditions. Examples of photoperiodism are discussed in relation to this.

The 'storm' stimulus (fast-falling temperature and/or breaking of water stress) stimulates anthesis in representatives of several families of flowering plants.

The flowering of evergreen forest trees (e.g. Dipterocarpaceae) at irregular intervals is attributed to preceding periods with large diurnal temperature ranges and high maximum temperatures indicating high insolation (which is probably the main inductive factor, because of consequent biochemical conditions associated with accumulation of assimilates and high carbohydrate status). Such flowering is thus not attributed to drought.

Flowering in many deciduous trees follows leaf-fall and/or new leaf appearance. Floral initiation may occur during a period when the tree bears only senescent leaves. Leaf abscission, and thus subsequent emergence of new leaves and flowers, appears to be a response to drought. Susceptibility to dry periods in particular seasons, more than in others, may be due to lack of response by new leaves not yet 'hardened' which results in an insensitive period, followed by a phase in which senescence is accelerated by photoperiodic conditions. In this last phase the foliage is sensitized.

Following the discovery of vernalization by the chilling of germinating seed (Gassner, 1918) and of photoperiodism or the effect of daylength (Garner and Allard, 1920), the environmental stimuli operative in many flowering plants of the temperate regions have become evident. How they operate is still being investigated. Considerable confusion has arisen in the past through the assumption that the flowering hormone was the same in all plants, or at least in large groups of plants, such as all 'short day' or all 'long day' plants or all those requiring vernalization. Various schemes were proposed to account for all the known effects of environmental stimuli on the synthesis and action of the hypothetical flowering hormone throughout these large groups of plants. These schemes were usually complicated and new exceptions to each improved scheme constantly arose. One common factor is evidently the derepression of genes (Wellensiek, 1969) even if the pathways to this differ.

The Humid Tropics

The humid tropics were delimited by Garnier on climatic criteria and by Kuchler according to the vegetation (Fosberg, Garnier and Kuchler, 1961). Both recognized constantly humid and seasonally humid region, and agreed that Malaya,

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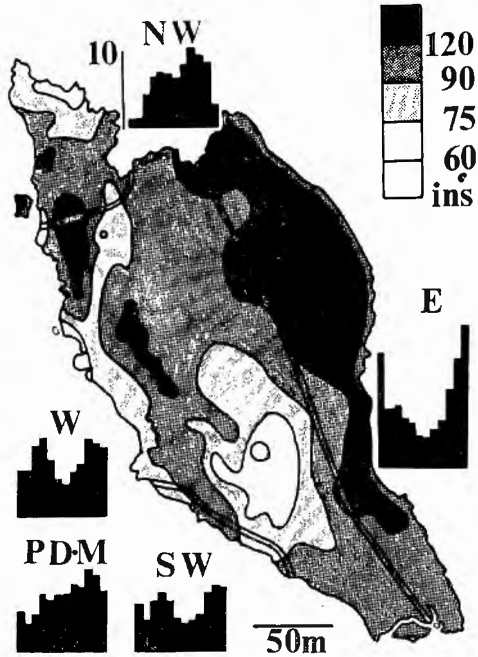

Fig. 1. Median rainfall in West Malaysia. Scale of histogram is 10 inches. Scale of map is 50 miles. NW North West Rainfall Region, W West Region, PD–M Port Dickson—Muar Region, SW South West Region (not demarcated) and E East Rainfall Region. The histograms are for NW Kangar, W Kuala Lumpur, PD—M Port Dickson, SW Kuala Pilah and E Pekan.

Sumatra, Borneo and most of Java (especially the western end) are in the 'true' ever-humid tropics.

The examples discussed below are as far as possible taken from this or similar equatorial regions, in which prolonged dry spells are rare, and annual precipitation usually exceeds evaporation. Figure 1 is a median rainfall map for West Malaysia. Here, potential evaporation is about 6 inches per month or 72 inches per year. The diurnal variation in temperature (mean maximum minus mean minimum) exceeds the seasonal variation (highest monthly mean minus lowest monthly mean). Figure 2 illustrates the monthly minimum, 24 hour mean and maximum temperatures for Kuala Pahang (coastal)and Ipoh (inland) in West Malaysia with small and large diurnal temperature ranges respectively. Many authors remark on the lack of seasonal variation apart from differences between wet and very wet periods.

Photoperiodism

Jagoe (1952) demonstrated that some varieties of rice (*Oryza sativa*) were sensitive to the relatively small differences in daylength in Malaya. Maturation (transplanting to flowering) was four to six weeks longer near the equator (2°16′N) than further north (6°08′N) when the plants were sown and transplanted on the

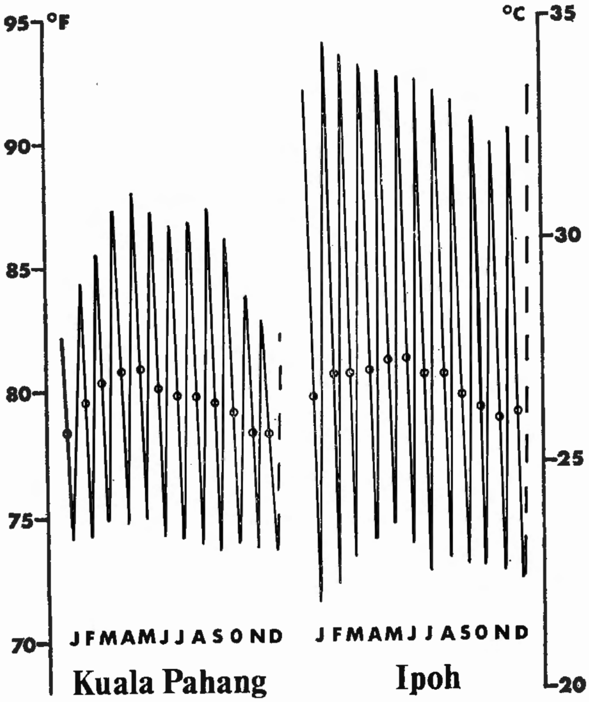

Fig. 2. Monthly minimum, 24 hour mean and maximum temperatures at Kuala Pahang and Ipoh, West Malaysia.

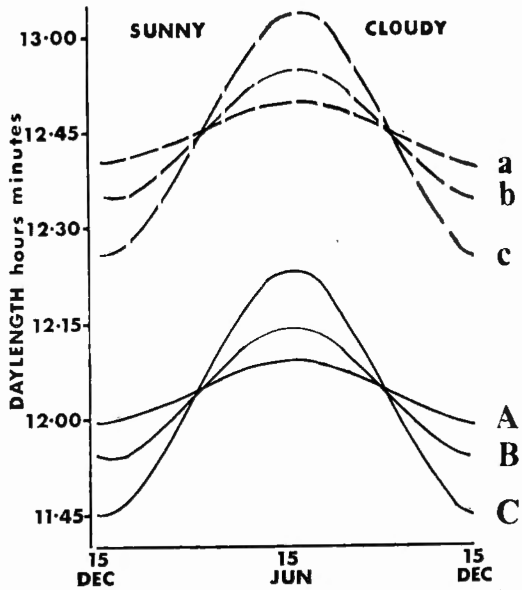

Fig. 3. Lower curves, official daylight. Upper curves, maximum possible daylight. A, a Singapore; B, b Kuala Lumpur; C, c Alor Star.

same dates from July onward in carefully controlled and irrigated plantings at eight stations. He confirmed that these were short day plants by experimentally delaying flowering by means of daylengths artificially extended by a short period.

Light was detectable (1 ft candle) for 7 to 20 (average 12) minutes before sunrise and for 12 to 22 (average 18) minutes after sunset, but light before sunrise was generally a little brighter than after sunset. Therefore the photoperiodically effective daylength was probably at least 20 or an average of 30 minutes longer than official daylight from sunrise to sunset. The data in Figure 3 were taken from Jagoe (1952). The lower curves are the periods of official daylight at Singapore (1°18′N), Kuala Lumpur (3°08′N) and Alor Star (6°09′N), taken from *The Nautical Almanac*. The upper curves are the maximum possible photoperiods obtained by adding 40 minutes to the lower curves. Since it is usually sunny (maximum hours of bright sunshine) during the early part of the year and more cloudy in the later part, the photoperiodic effect is probably intensified.

Table 1. Monthly means of percentage cloud and hours of bright sunshine per day for all stations available in Malaysia with their standard errors.

	J	F	M	A	M	J	J	A	S	O	N	D	MSD (5%)
% cloud	73.6	65.6	69.4	71.7	72.4	74.1	73.8	76.6	78.4	82.0	79.8	77.1	2.2
s.e. ±	0.93	1.32	1.20	1.22	1.56	0.83	0.82	0.99	0.84	0.69	0.72	0.88	
Hbs/d	5.92	7.37	6.92	6.97	6.75	6.54	6.55	6.30	5.85	5.31	5.12	5.26	0.27
s.e. ±	0.235	0.185	0.179	0.202	0.133	0.108	0.109	0.115	0.118	0.127	0.145	0.188	

The Minimum Significant Differences ($P < 0.05$) are based on the interaction of the months × stations

The monthly means of various meteorological data for 5 year periods at up to 27 stations in Malaysia (nine of them duplicated for different five year periods) were given by Wycherley (1971). The overall averages of percentage cloud and hours of bright sunshine are given in Table 1. Despite the lack of close coordination between the cycles at different stations (see for example the curves for sunshine in Figure 5), the means show a marked seasonal variation likely to result in a cycle of effective photoperiod which therefore is long early in the year and short later; that is, approximating to curves 'a', 'b' and 'c' of Figure 3 during the early part of the year and to 'A', 'B' and 'C' during the latter.

Dore (1959, 1960) confirmed Jagoe's observations and showed that increasing daylength from 11 hr. 50 min. to 12 hr. 20 min. increased the period from sowing to ear emergence in *c.v. Siam 29* from 90 to 150 days. He showed that differences in daylength of as little as five minutes were effective in the critical range. Njoku (1959) reported similarly for *O. sativa* and *O. glaberrima* at Ibadan, Nigeria, (7°26′N).

It is likely that effects similar to those in rice could be demonstrated in photoperiodically sensitive varieties of soybean (*Glycine max*) and other annual grain legumes (e.g. *Phaseolus* spp.) in Malaysia, because the period from germination to harvest seems to vary with latitude and sowing date.

Flowering and red pigmentation are promoted in *Euphorbia heterophylla* by short days (Garner and Allard, 1923). The closely related shrubby perennial *Euphorbia pulcherrima* ("poinsettia") has been observed (Wycherley, unpub.) in Kuala Lumpur (3°08′N). The foliage is mainly green, and vegetative growth occurs in the middle of the year. Towards the close of the year much of the foliage is pigmented red and there is profuse flowering. There are usually a few green and a few red leaves to be found at any time of year, but the general trend is well marked. A potted plant illuminated at night under a security lamp remained green indefinitely. This is attributed to the extended daylength, but might be an effect of potting; however, potted plants with bright red foliage have been seen elsewhere.

At Cameron Highlands (4°30′N and 5000 ft elevation) the range in pigmentation of *Euphorbia pulcherrima* is from pink in July to scarlet in December. This is probably due to further reduction in the effective day-length due to heavy cloud (the mean hours of bright sunshine at Tanah Rata are about three-quarters of those at Kuala Lumpur). It is possible that the lower temperatures in the hills have a modifying effect (apart from possible genetic differences) but this is unlikely because Garner and Allard conducted their experiments on *Euphorbia heterophylla* at about 39°N.

Triggering of Anthesis

A large number of tropical plants open their flowers gregariously. In many of these the flower buds are differentiated, but their development is arrested and they remain dormant until released by an appropriate stimulus. All buds, which had reached the stage of development at which arrest occurred, then develop and reach anthesis together. In some species the flower buds are not visible macroscopically at the time of the stimulus, which may in these cases be responsible for floral induction or the initiation of flower buds as well as their simultaneous development and opening.

Coffee is one of the best known and studied examples. Piringer and Borthwick (1955) showed that short days of less than 13 hours initiated flower bud formation in *Coffea arabica*. Alvim (1960) compared regularly irrigated bushes, in which anthesis was suppressed indefinitely, and those allowed to develop water stress almost to the wilting point. In the latter, but not the former, artificial watering or rain caused anthesis of many flowers 10–11 days later. Van der Veen (1968) found that 1% gibberellic acid could bring on anthesis in 10 days, but auxin and kinetin were not effective, whereas 200 ppm abscissic acid inhibited flowering in plants whose water stress had been broken.

The breaking of water stress may not be the only environmental factor. Rees (1964a) studied *Coffea rupestris* near Benin, Africa (6°53′N). The main flowerings occurred from early January to mid-April and each was three days after heavy rain or artificial watering of a bush growing under natural unirrigated conditions. A regularly irrigated plant flowered sparingly except for heavy flowering after light showers, which produced no response in the unwatered plant. Rees agreed floral initiation was probably by short days and that the breaking of water stress, if present, was an adequate stimulus for anthesis. He resolved the anomalous effects of light showers by assuming that they were inadequate to break water stress in unwatered plants, while in watered plants, in which no water stress had developed, the stimulatory effect of the light showers was due to rapid cooling as shown in the temperature records.

Sudden Cooling

The sharp drop in temperature during tropical rain storms was first shown to stimulate simultaneous anthesis in those orchids which bear ephemeral flowers lasting only one or two days, notably *Dendrobium crumenatum*. Burkill (1917) noted that heavy rain eight days earlier seemed to be the trigger, although he queried if it was the rain itself or the induced temperature changes. Seifriz (1923) analyzed the dates of anthesis of *D. crumenatum* and the rainfall data at Bogor, which showed a very high correlation between flowering and heavy rain eight days earlier. Meteorological instruments are usually read in the morning, so that the amount of rain entered against a given date actually fell in the 24 hours preceding the time of reading the gauge on the morning of that date.

Smith (1926) noted that artificial watering of orchids either in the open or under glass and protected from direct rain did not induce flowering or different behavior from those growing wild in the vicinity. He commented that nearly 60 Malesian orchids had ephemeral flowers and that 12 of them definitely flowered gregariously; of these, seven reached anthesis the day before *D. crumenatum*, three more on the same day and *Thrixspermum raciborskii* a day later. Burkill (1918) recorded simultaneous anthesis in *Saccolabium calceolus*, usually just before flowering of *D. crumenatum*.

Experiments with *D. crumenatum* and *Thrixspermum arachnites* by Coster (1925, 1926) confirmed that the temperature drop of 5–8°C during the rain storm was the main inductive factor. There was no flowering if the plants had been protected in a warm room during the storm. Cooling for several hours in a water bath at 20°C induced anthesis after the characteristic interval. The rise in humidity associated with the drop in temperature was not a factor, because plants chilled over a strong desiccant flowered anyway. Meteorological data showed that rain produced a greater or more rapid drop in temperature and was a more effective stimulus of flowering if it fell during a dry period when evaporation and heat loss were greater, whereas rain at night when the atmosphere was saturated was ineffective.

A large collection of *Dendrobium crumenatum* was observed in Kuala Lumpur from mid- 1961 to late 1964, except for a long period in 1962 and shorter periods at other times. The collection included plants of 12 distinct provenances: Arau, Perlis; Bedong, Kedah; Bogor, Java*; Kajang, Selangor; Kampar, Perak; Karak, Pahang*; Kuantan, Pahang; Pulau Angsa*; Scudai, Johore; Seria, Brunei*; Singapore*; and local Kuala Lumpur plants. (Those marked* were obtained through

Mr. H. M. Burkill, then Director, Botanic Gardens, Singapore). A total of 27 flowering dates were recorded. The local plants flowered on 18 of them, the introductions on 22; 13 dates were common to both local and introduced plants; the local plants flowered five times when none of the introductions flowered; and at least one of the introductions flowered on nine occasions when no local plants flowered. These discrepancies were more numerous in the early stages than later and were attributed to the introduced plants needing a period in which to get in phase with the local plants the production of susceptible buds and their elimination by opening.

Examination of rainfall and thermohygrograph records confirmed that rain fell during the day and caused a drop in temperature and rise in humidity usually nine days before anthesis (that is eight meteorological record days). Occasionally a few buds opened a day later than the majority, and sometimes a single flower opened on the tenth day. If general flowerings only are considered, then the number of days from storm to anthesis is 9.0±0.00. For the introductions flowering on their own the mean period was 9.47±0.14 days, but this was reduced to 9.20±0.14 if the stragglers flowering one day after the rest were eliminated.

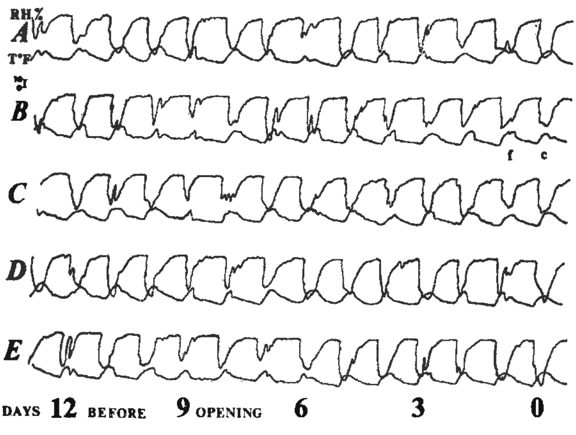

Fig. 4. Traces of thermograph records in vicinity of *Dendrobium crumenatum*. Upper trace is of Relative Humidity % and the lower is of Temperature °F. The scale indicates 10 units, i.e. 10% RH and 10°F. f = flowering of *D. flabellum* one day before c = *D. crumenatum.*

Examples of the thermohygrograph records are given in Figure 4. In the examples B and E, it is difficult to explain why the earlier more rapid falls in temperature were not effective. Perhaps the buds were not yet susceptible or these earlier stimuli sensitized the buds to respond to lesser stimuli later. The mean drop in temperature for general flowering was 12.3±0.75°F or a rate of 0.147±0.0200°F per minute. The corresponding figures for the introductions were 12.7±0.93°F and 0.198±0.0361°F/min.

The introductions fell into three groups for frequency of flowering. Most frequent, apart from the local plants, were Kajang, Pulau Angsa and Singapore;

moderately frequent, Arau, Bedong, Kampar and Karak; infrequent, Bogor, Kuantan, Scudai and Seria. Some of the plants were bigger than others, although these were not always the most prolific or frequent in flowering. It was not possible to determine from the limited records if there was any variation in their susceptibility to or requirement for stimuli of different intensity; there was no clear pattern relating behavior to provenance. The most prolific flower-bearers were from Kampar, Pulau Angsa, Scudai and Arau.

A plant of *Dendrobium flabellum* flowered eight times, six times one day before *D. crumenatum* flowered, once two days before, and once quite independently. The mean period from stimulus to anthesis was 7.7 ± 0.17 days. This confirms the findings of Burkill and Smith. The mean temperature drop was 11.0 ± 0.66°F and the rate was 0.126 ± 0.0224°F/min.

Gradual Cooling

Under natural conditions the drop in temperature during a storm by day is sudden, but the minimum temperature so attained is seldom as low as that which is gradually reached every night. Investigation under experimental conditions by Kerling (1941) showed that if plants of *D. crumenatum* or *Zephyranthes rosea* were kept at night temperature in a cool room at dawn and through the following two days, this prolonged exposure to cool conditions gradually attained was as effective in producing anthesis as a much smaller and briefer but sudden drop in temperature. Holttum (1953) remarked that a day during which the temperature never exceeded 80°F (26.7°C) was effective. Such a cool day would be a wet day, as also would be a stormy day, so that the water for bud expansion would be available. Coster (1926) found a nearly twenty-fold increase in dry weight of the flower-buds but a 60 to 70-fold increase in fresh weight, the absolute water content increasing 70 to 85-fold from resting stage to anthesis. Kerling showed also in *Z. rosea*, a bulbous plant, that not only was sudden or prolonged cooling necessary, but a small amount of water must be present. However, water stress was not a prerequisite and breaking of water stress was not a substitute for cooling.

Holttum (1949) found that buds of the orchid *Bromheadia finlaysoniana* took 20–30 days, average 25, to open from when first visible. The buds developed uniformly until 12–30 mm long, when a retardation set in. A cool day, but not necessarily a sudden cooling as in a storm, seemed to trigger an acceleration of growth leading to simultaneous flowering seven days later. As a result there was irregular gregarious flowering at intervals of 6–12 days, each flower itself lasting only one day.

De Vries (1953) concluded that a period of two to three weeks with night temperatures of 19–21°C was necessary to induce flower initiation in *Phalaenopsis schilleriana*, but no specific conditions were necessary to trigger anthesis. This orchid has more persistent flowers than those discussed above.

Clerodendrum incisum (Verbenaceae) was found to combine several of the above features (Rees, 1964b). Gregarious anthesis followed 25–35 days after (i) heavy rain during the wet season, (ii) almost any rain during the dry season or (iii) a cool period in the absence of rain. The first two were equated with sudden cooling and the last with prolonged cooling. The buds were not visible macroscopically at the time of the stimulus. This may be more a case of floral initiation rather than of triggering anthesis.

Gregarious flowering at some interval after the storm stimulus (whether this be temperature drop or breaking water stress) has been reported in *Pterocarpus indicus, Randia macrantha* and perhaps *Palaquium obovatum* (Corner, 1952), *Epiphyllum oxypetalum* 24–25 days (Holttum, 1953) and *Murraya paniculata* cv. *exotica* 14–15 days (Coster, 1926). Thus the phenomenon occurs in its general form, even if not definitely in detailed mechanism, in the Amaryllidaceae, Cactaceae, Leguminosae, Orchidaceae, Rubiaceae, Rutaceae, Sapotaceae and Verbenaceae, including both monocotyledons and dicotyledons. Most, if not all examples of these gregarious, ephemeral flowers are scented. There are obvious advantages in simultaneous flowering and attractive scent in cross-pollinating plants with short-lived flowers. Alternatively, if periodic gregarious appearance of attractive flowers has evolved, there may be no need to retain continuous flowering or persistence in the blooms. Whatever the evolutionary history and significance, this phenomenon is widespread geographically and phyletically in the tropical flora.

Gregarious Flowering of Forest Trees

A distinction must be made between the evergreen trees and the deciduous trees (Holttum, 1930, 1940, 1953). Healthy evergreen trees are never bare, and new foliage may appear in flushes or continuously. The bearing and opening of flowers appear for the greater part to be independent of changes in the foliage. On the other hand deciduous trees usually lose their old leaves either from some branches or often from the whole adult tree all at one time, so that it is partly or completely bare. New leaf may emerge before the old has fallen, or (perhaps more commonly) after a leafless period. In deciduous trees flowering is usually associated with some phase of the defoliation and refoliating cycle, usually immediately before or after the emergence of new leaf. Thus if the factors controlling leaf change can be determined in most deciduous trees, the relationship of their flowering to the seasons becomes largely self-evident.

This is not so in the evergreen trees. The Dipterocarpaceae illustrate gregarious flowering on a grand scale. Wood (1956) remarked that the interval between flowerings was 2–9 years in Sabah and 9–21 years between heavy flowerings. The heavy flowerings which began in November 1924, June 1934 and April 1955 extended all over Sabah and perhaps further afield. Similar experience has been reported by foresters in all territories in the region. Although the swamp, lowland and hill dipterocarps do not seem to be in phase but display somewhat different cycles or periodicity, the inference is inescapable that millions of trees of different ages and of dozens of species flower more or less simultaneously at irregular periods of several years over areas of thousands of square miles.

Despite the colossal scale of this phenomenon and its significance in forestry for improved or selective regeneration, there is little data available for analysis. Contemporary meteorological records are often lacking or incomplete. Wood (1956) was unable to find any support for the hypothesis that flowering of dipterocarps followed a particularly dry year or month. He gave the production of Illipe-nuts each year from 1914 to 1955 in Sabah. J. A. R. Anderson communicated (1966) the export of these nuts (in tons) from Sarawak for 1908 to 1965 (omitting 1941–45).

The Illipe-nut comes from *Shorea macrophylla* (*S. gysbertsiana*) and certain related hill Dipterocarpaceae. In much of Sarawak the less wet season comes about the middle of the year (in some central and eastern districts there is a tendency towards two less wet periods before the equinoxes). According to Anderson (1966) flowering usually occurs in September or October (thus following a less wet period) and fruit ripens in January to March of the following year.

Table 2. Export of illipe nuts from Sarawak and average meteorological data for Bintulu, Kuching and Miri.

Year	Nuts exported tons	Rainfall inches	Diurnal temp. range °F	Maximum temp. °F
1947	7658	134.72	—	—
1948	22	132.53	—	—
1949	752	151.74	—	—
1950	—	130.13	14.5	87.8
1951	22	133.21	14.4	88.1
1952	30	143.66	14.2	87.8
1953	2807	132.17	15.1	88.4
1954	16047	155.80	15.1	88.0
1955	1452	158.20	14.9	87.6
1956	158	148.10	14.2	87.0
1957	—	132.07	14.2	87.6
1958	6205	131.55	14.1	87.8
1959	22006	131.06	13.9	87.2
1960	—	132.95	14.4	87.7
1961	15	132.29	14.5	87.7
1962	19883	154.80	13.8	87.1
1963	—	165.19	13.3	86.8
1964	—	151.12	14.0	87.3
1965	500	125.03	14.8	87.5
1966	1000	143.68	14.7	88.2

A preliminary analysis has been made of the Sarawak illipe-nut production, compared to rainfall (1947–66) and temperature (1950–1966) data. The meteorological records for Bintulu, Kuching and Miri were averaged, (Table 2). Production is not a measure of flowering alone, because the actual production will depend on the maturation of the fruit as well. No correlation was found between nut production and the meteorological data for the same year, but since the latter refer largely to conditions after the fruit have been harvested, this result is not unexpected, but confirms that there is no chance coincidence of different cycles. The correlations between production and conditions the year before and the year before that were then analysed. Only the correlations between production and the year immediately prior were significant in any degree.

The logarithm of production was used in regression analysis, treating zero production as one ton (i.e. logarithm = 0.0).

A negative correlation ($r = -0.400$, $P < 0.1$) was found between production and the total rainfall during the previous year, which was in the range 125–165 inches (3175–4190 mm) per year, indicating a ratio of precipitation to evaporation of at least 2, probably more. The correlation between production and the rainfall during the month with the lowest rainfall during the previous year was not significant ($r = -0.216$). This argues against an especially dry spell being the stimulus. The range in rainfall during the driest month was from 0.85 to 6.80 inches (22–173 mm).

The correlations of the following temperature variates during the previous year with the production were analyzed:—the annual mean minimum, the annual mean maximum and the difference between them, which is the annual mean diurnal temperature range; the lowest and highest monthly mean minimum and maximum temperatures. In ascending order of significance the following correlations were obtained between production and the previous year's:—lowest monthly minimum ($r = -0.432$, $P < 0.1$), 70.4–72.8°F (21.3–22.7°C), annual mean diurnal temperature range ($r = +0.551$, $P < 0.05$) 13.3–15.1°F (7.4–8.4°C) and annual mean maximum ($r = +0.676$, $P < 0.01$) 86.8–88.4°F (30.2–31.3°C). The diurnal temperature range has been found to be significantly correlated with solar radiation at any station in Malaysia (not between stations), (Wycherley, 1971). This and the negative correlation between production and total rainfall during the preceding year suggest that the amount of insolation is the physiologically important factor determining the yield of nuts, even if not necessarily of the flowering. Higher maximum temperatures are attained during periods of longer insolation, and since conditions favor back-radiation at these times, the lower minima are also consistent with this explanation.

Malayan data on fruiting of the Dipterocarpaceae are mainly qualitative. Barnard (1954) gave the fruiting years for Malacca as 1929, 1931, 1933, 1935 and 1938 and for Selangor as 1931 and 1933, Boswell (1940) added 1938 and to a lesser extent 1939 for Selangor. The monthly rainfall data averaged for five stations in each of the states of Malacca and Selangor during these periods are given in Table 3. It was not indicated if fruiting was early or late in the various years. Flowering and fruiting may have been initiated by the dry months indicated in bold-face in Table 3, but if so it is surprising that some of the dry months indicated in italics were not also effective.

A series of reports by the Forest Department (1949–1958) and by the Forest Research Institute (1959–1967) permits an approximate account of fruiting by

Table 3. Monthly rainfall in inches in Malacca and Selangor.
Malacca (average for Bukit Asahan, Bukit Lintang, Lendu, Rembia and Tebolang Estates)

Year	J	F	M	A	M	J	J	A	S	O	N	D	Annual
1932	3.91	4.48	5.64	7.76	4.01	4.67	6.21	4.26	6.70	7.40	13.00	**3.34**	71.53
1933*	6.06	**3.18**	7.60	8.40	8.91	5.63	8.73	7.52	8.19	6.81	8.64	8.37	88.03
1934	10.38	*2.37*	11.25	7.81	4.71	5.72	6.84	5.27	**3.48**	13.27	12.79	**3.72**	87.60
1935*	**3.08**	**4.05**	7.43	5.47	7.32	7.45	7.65	9.38	4.50	12.89	9.17	9.44	87.84
1936	6.25	4.02	6.07	8.83	7.70	4.38	7.49	9.34	5.13	11.58	11.09	8.99	90.87
1937	5.32	*3.59*	8.10	10.23	5.24	4.58	6.58	5.89	9.42	9.75	8.00	10.18	86.87
1938*	4.47	**0.80**	10.03	9.37	6.85	**2.55**	4.56	7.77	6.16	10.75	7.16	9.05	79.51

Selangor (average North Hummock, Sedgely and Tennamaram Estates,
Ampang Intake and Kuala Kubu Bahru)

Year	J	F	M	A	M	J	J	A	S	O	N	D	Annual
1930	8.85	*2.48*	6.07	10.86	4.64	8.94	**1.93**	6.30	4.44	17.62	10.12	8.15	90.40
1931*	12.73	**3.58**	9.13	10.85	9.46	6.69	8.10	*3.40*	9.77	7.10	11.75	11.93	104.50
1932	5.25	5.72	11.40	9.87	8.67	5.38	4.66	10.73	8.33	13.82	13.62	8.14	105.59
1933*	7.52	7.31	12.83	12.66	13.74	**3.06**	6.11	9.62	9.13	8.21	8.90	10.55	109.64
1934	10.06	*3.12*	13.61	12.71	6.93	11.18	5.03	7.54	7.01	10.46	12.42	5.32	105.39
1935	5.76	7.07	9.26	10.93	6.39	7.18	*3.32*	9.58	8.01	13.19	14.03	14.27	109.40
1936	8.48	5.22	9.69	11.25	14.31	5.28	*2.07*	5.99	8.53	11.87	11.20	8.53	102.44
1937	8.84	5.48	10.72	11.05	6.45	*2.82*	5.44	3.72	6.99	11.39	11.97	9.48	94.35
1938*	5.88	4.55	11.84	10.03	10.54	**1.41**	**3.45**	8.31	6.25	12.34	8.25	8.33	91.19

*Fruiting of Dipterocarpaceae

Table 4. Fruiting of Dipterocarpaceae in Selangor and the estimated average meteorological conditions for Kajang and Kepong during the previous year (July to June except January to December for first half 1959).

Year	Fruiting	Annual Rainfall Inches	Diurnal Temperature Range °F Annual	Diurnal Temperature Range °F Greatest Monthly
1948	None	110.0	18.24	20.05
1949	Good	95.8	18.30	20.45
1950	Poor	111.0	17.60	19.60
1951	Bad	99.9	17.73	21.15
1952	None	120.5	18.26	18.90
1953	None	104.2	18.26	19.40
1954	None	100.9	17.56	19.20
1955	Good	87.4	18.43	20.75
1956	None	93.2	18.59	20.00
1957	Excellent in August and December	100.4	18.97	22.40
1958	Good in October and November	112.4	19.02	21.40
1959	Fair in January and February	92.0	19.43	21.40
	Poor in July and August	91.1	19.29	21.85
1960	Poor	96.0	18.61	20.60
1961	Fair in Second half	95.8	18.46	21.05
1962	Poor	88.7	18.73	20.80
1963	Good in second half	78.6	19.11	21.80
1964	Poor	101.6	18.39	19.80
1965	Fair	91.9	18.02	20.10

Dipterocarpaceae in Selangor as shown in Table 4. It was suggested in the F.R.I. Annual Report for 1957 that a dry spell of two to four weeks initiated flowering and fruiting about six months later. These dry spells usually occurred in February, or June and July, so that fruiting was observed in the second half of the year or early the next. Although the north-east monsoon almost failed in late 1958, there was less fruiting in 1959 than expected, and the hypothesis was modified that good fruitings were unlikely in successive years, some recovery period being necessary. Even so, good fruitings were obtained twice in 1957 and again in 1958.

The meteorological records of Selangor for the period 1947 to 1965 are fragmentary. The main station was moved when the airport site was changed. However, some temperature and rainfall records are available for every month for either Kajang or Kepong, and for many months for both. By regression analysis the missing data have been estimated and average data for Kajang and Kepong have been calculated.

The fruiting has been scored on a scale of 0 (none) to 5 (excellent) and correlated with the meteorological data during the year from the previous July to the current June, because most fruiting occurred in the second half of the year, except for the fair fruiting in early 1959, when the meteorological data for the calendar year 1958 were used. Correlations with the following were attempted:—the annual mean, the lowest and the highest monthly values during the previous year of the rainfall, number of rainy days, minimum temperature, maximum temperature and diurnal temperature range.

In ascending order those which showed any significance were:—lowest number of rainy days in a month ($r = -0.389$, $P < 0.1$) 4–13 days, mean number of rainy days per month ($r = -0.405$, $P < 0.1$) 12–17 days, annual rainfall ($r = -0.415$, $P < 0.1$) 78.6–120.5 inches (1997–3062 mm), annual mean diurnal temperature range ($r = +0.478$, $P < 0.05$) 17.6–19.4°F (9.8–10.8°C) and the highest monthly mean diurnal temperature range ($r = +0.719$, $P < 0.001$) 18.9–22.4°F (10.5–12.4°C). There was no evident correlation between fruiting and dry spells as indicated by low monthly rainfall, and only very weakly as indicated by the number of rainy days.

Admittedly the official meteorological records obscure those dry spells which occur in more than one calendar month. Nevertheless annual rainfall gives a slightly better negative correlation than the driest month and the positive correlation with the annual mean diurnal temperature range is significant. The greatest monthly diurnal temperature range gives a highly significant correlation. Thus these Selangor results agree with those from Sarawak.

This does not explain fully however, the gregarious flowering of the Dipterocarpaceae, although further doubt is expressed about water stress being the stimulus. Workers who disagree that temperature and insolation are the stimuli point to the comparatively small ranges involved. However, although the differences from year to year are small, they are statistically and physiologically highly significant, because they are operative for long periods. The status of carbohydrate reserves may be affected critically by higher insolation and assimilation or by lower night temperatures and reduced respiration.

The technique of 'crop logging' has demonstrated a number of correlations between yield and environmental conditions. For example Hord and Spell (1962) found highly significant negative correlations between days to maturity in banana and the mean temperature or hours of bright sunshine over the same period. Sparnaaij, Rees, and Chapas (1963) found highly significant correlations between the weight of bunches per oil palm and the effective sunshine (actual sunshine modified by a factor for water deficit during the dry season) for the period 28 months earlier. The percentage of fruitful buds on sultana (*Vitis*) vines was found by Baldwin (1964) to be closely correlated with the hours of bright sunshine and the sum of the daily maximum temperatures (between 82 and 90°F) over a period of three weeks during late spring. May (1965) showed that inflorescence formation was reduced in the sultana vine by shading individual buds.

Several examples are quoted by Jackson and Sweet (1972) of the general tendency of shade to depress flower initiation and of high light to increase it, irrespective of photoperiod. High temperature is variable in its results according to species. Also flowering is often associated with high carbohydrate levels, although there is little evidence of any direct role. Probably flowering is associated with some biochemical condition which is in turn associated with high carbohydrate levels. Something of this nature seems to be involved in the case of the Dipterocarpaceae. In discounting moisture stress as such, the frequent but not invariable coincidence of drought and high insolation may account for apparent cases of causal relationship. Moisture stress may yet play some role in co-ordination of flowering in trees 'ripe to flower' owing to high insolation.

Seasonal Leaf Change and Flowering

Definite seasonal leaf change and associated flowering are best known in those parts of the country with a monsoon climate. *Hevea brasiliensis*, the para rubber tree, is an introduction from another humid equatorial region. In mature trees the leaves fall and the inflorescences are borne in the axils of scale leaves and the lower foliage leaves proximal on the new shoots, which elongate immediately after the brief period when the trees are bare. Defoliation is most intense and regular in north west Malaya in the rain shadow of the north east monsoon (Wycherley, 1963). In Singapore the mean period between leaf changes of *H. brasiliensis* was found to be 13.3 months over nearly 15 years (Holttum, 1940). The departure from exactly 12 months probably reflects the more uniform climate and the less regular appearance of the dry spell early in the year.

There is a second flowering of *H. brasiliensis* on new shoots produced in August and September following the usually dry month of July, but this second flushing of new shoots and flowering is not usually preceded by defoliation. Nevertheless it is fairly regular and used by plant breeders for pollination.

The wild *Elateriospermum tapos* (Euphorbiaceae), native in Malaya, has its young leaves red and most spectacular. McClure (1966) observed four trees for five years in Ulu Gombak (3°20′N) and found that they defoliated, bore flowers on the bare twigs and refoliated regularly and uniformly together each year during late January to early April. Corner (1952) has suggested that, like *H. brasiliensis*, there is sometimes another flowering of *E. tapos* after the dry spell in July and that it is evergreen or irregular in its behaviour in south Malaya.

Six deciduous trees (some of exotic origin) with annual leaf renewal and three with six-monthly periodicity in Singapore were listed by Holttum (1940). There were also nine species with periods of more than a year and ten with periods between 6 and 12 months, and about six other deciduous trees irregular in their behavior. At Ulu Gombak seven species (all native including *E. tapos*) had fairly regular annual cycles of leaf change, flowering and fruiting apparently following the dry spell early in the year (McClure, 1966). Another seven species displayed fairly regular cyclic behavior, but these were apparently independent of dry spells and the intervals differed considerably from 12 months. Behavior in the other 18 species was more or less irregular.

Most observations and circumstantial evidence agree that the dry spell which commonly occurs early in the year throughout Malaysia triggers leaf change ('wintering' in rubber) and the associated flowering in deciduous trees. The onset of the phenological phenomena is early or late according to the date and intensity of the dry spell. The driest month throughout Malaysia as a whole and at many stations is July, yet this seldom stimulates such marked responses.

Annual Climatic Cycles

Rainfall records are available for longer series and more stations than other meteorological data and have tended to dominate any discussion of phenology. Malaya has been divided into rainfall regions with monomodal and bimodal seasonal rainfall distribution (Dale, 1959); so also has East Malaysia (Wycherley, 1967). Sunshine, measured as hours of bright sunshine or the percentage possible, or more recently as radiant solar energy, shows a well marked cycle in most parts of Malaya.

Sunshine is lowest in October to January and highest in January to April. The cycle is more or less monomodal at many stations, although showing a tendency towards a second peak in July or August in some. The convectional rains of April and May, which usually fall late in the day, are not associated with so marked a depression in sunshine as the more continuous monsoon rains late in the year. The cycle is in advance on the west coast and about two months behind on the east coast. The amplitude of the variation is dampened in the south, particularly in Singapore, where a bimodal seasonal distribution is more evident.

Other meteorological phenomena depend largely on sunshine. The probable modification of the effective photoperiod has already been mentioned.

Abscissin II, the growth inhibitor, production of which in birch and sycamore is increased by short days, has been identified by Cornforth, Millborrow, Ryback and Wareing (1965). Although Chua (1970) was unable to detect seasonal differences in the absolute level of abscissic acid in leaves of *Hevea*, there was an increase relative to auxin (which fell) associated with the onset of senescence towards the end of the year. The days shortened by astronomic and meteorological conditions late in the year may accelerate processes of foliar senescence, so that the leaves

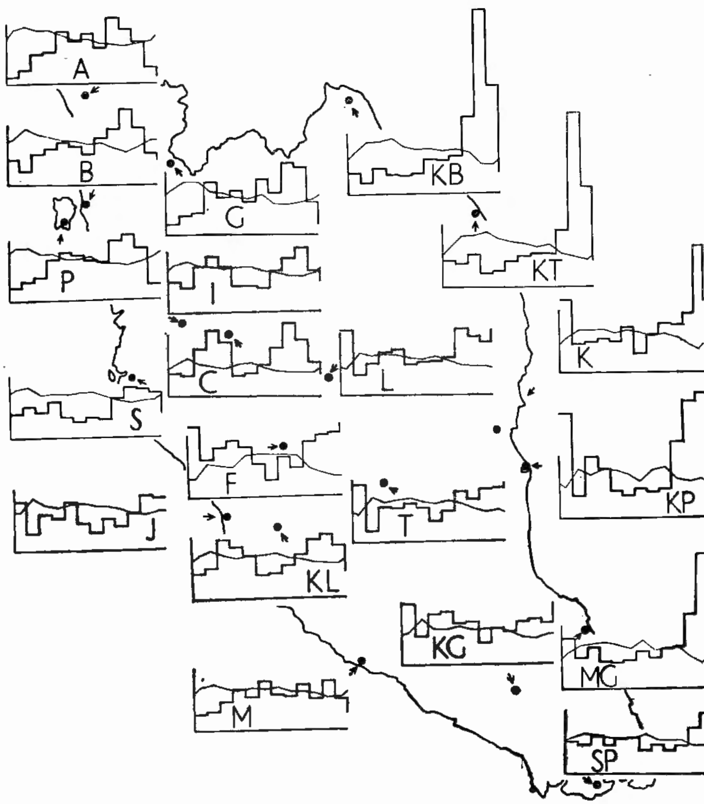

Fig. 5. Monthly mean rainfall in mm/day as histograms and monthly means hours of bright sunshine per day as curves. The vertical axis in each diagram corresponds to 10 mm/day and 10 hrs/day. The horizontal axis indicates the months January to December. A Alor Star, B Butterworth, S Sitiawan, J Bukit Jeram, G Grik, I Ipoh, C Cameron Highlands, F Bukit Fraser, KL Kuala Lumpur, M Malacca, KB Kota Bharu, KT Kuala Trengganu, L Kuala Lipis, T Temerloh, KG Kluang, K Kuantan, KP Kuala Pahang, MG Mersing, and SP Singapore. All are the means for 5 years except for Grik which is for 2 years only.

are more susceptible to dry conditions triggering their abscission in the early part of the year than in mid-year.

As the hours of bright sunshine lengthen so the maximum temperature increases, this in turn causing more back-radiation (the rate of cooling is proportional to the temperature) and the diurnal temperature range increases also. The maximum temperature curve lags a little behind the insolation curve, but the latter and that of diurnal temperature range are in phase. In the humid tropics the atmosphere is near saturation at night, and the minimum relative humidity by day is negatively correlated with the rise in temperature (diurnal temperature range). This is in phase with sunshine, as is potential evaporation. Therefore all factors which collectively contribute to drying, evaporation and water stress are associated with the variation in sunshine. Only the mean 24 hour and minimum temperature curves lag a little further behind those for sunshine and maximum temperature.

The pluvial and solar cycles are related to each other through cloud cover, but their variation is not completely correlated. The negative relationship between warm, drying conditions and rain is most pronounced early in the year when the phasing of the cycles is strongly opposed. The phasing of the cycles varies throughout the year and throughout the country (Figure 5). The second dry season is probably more important in Singapore, where the total rainfall is low and relatively evenly distributed.

Senescence

The usual life span of individual leaves before they become senescent is probably another important factor maintaining regular rhythmic phenology in deciduous trees. Schweizer (1932) artificially defoliated trees of *H. brasiliensis* at various periods before the date of expected leaf fall as determined by prior observation. Trees defoliated five months before the anticipated leaf fall 'wintered' as usual; but if defoliated two to three months before, the next leaf change was delayed up to three months. He suggested that five months was the minimum period for the leaves to become senescent and susceptible to the stimulus.

Chua (1970) investigated the changes in various constituents of leaves of *H. brasiliensis* from their expansion in April to their fall almost a year later. He also found differences in the reaction of the leaves to applied growth substances as they aged, at some stages accelerating and at others delaying abscission. Thus there are internal, largely age-dependent, factors involved.

The operation of these internal and external factors will tend to keep trees of the same species in the same area in phase together after responding to the earliest stimulus above the threshold level in any annual cycle. The new leaves will be insensitive for a period to even more intense stimuli. In some species this may carry them over the second dry spell in July. Cycling in phase will be accentuated if senescence is accelerated by the dull conditions in the later part of the year.

In the deciduous trees inflorescences are initiated in a definite relationship to leaf change. It may be inferred from the results of Chua (1970) with *H. brasiliensis* that the presence of senescent leaf alone on the shoots may be important in this respect. Young plants with leaf at all stages from newly expanded to senescent do not flower, unless senescence and abscission of all the foliage is artificially induced at one time.

Deciduous Habit in Equatorial Regions

The putative function or advantage of the deciduous habit in temperate (seasonally dull) and monsoon (seasonally dry) regions seems obvious, namely to discard the leaves when they might be below the compensation point or transpiring excessively. As Wright (1905) indicated, only those deciduous trees which remain bare throughout the period of water deficit can reduce transpiration appreciably by defoliation during the dry spell, e.g. *Bombax malabaricum* in Ceylon. The majority of deciduous trees in Ceylon and Malaya produce new leaves before the dry period ends.

The temperatures of leaves were determined by Smith (1909). The young, often pigmented and deflexed, foliage attained higher temperatures than the hardened green foliage in some cases, but lower in others, and presumably transpired more or less accordingly. No recent determinations of temperature or transpiration of such leaves were found during a brief search of the literature, but the subject probably deserves investigation by modern techniques. Smith suggested that refoliation with pigmented young leaves during a dry spell might ensure the maximum transpiration and hence translocation of mineral nutrients to the new shoots. It is doubtful if such a mechanism could raise transpiration much in excess of the potential evaporation, which does not vary greatly throughout the year in Malaysia (Wycherley, 1967, 1971).

In *Hevea brasiliensis* defoliation and refoliation during the dry spell is advantageous in escape of some leaf-diseases, (Ho, Ng, and Subramaniam, 1969) such as *Gloeosporium* which can only attack young foliage during wet weather. Rao (1971) demonstrated this by artificial defoliation. Although an agricultural advantage and perhaps a quasi-evolutionary advantage in a plantation, where conditions favor epiphytotic outbreaks of disease in populations of uniform age and genetic constitution, this may not apply in very heterogeneous, wild populations.

The deciduous habit, where it is associated with consequently coordinated flowering, may—like gregarious flowering in response to other more specific stimuli—reduce wastage of flowers and increase the chances of cross-pollination in mixed communities, where individuals of the same species may not be adjacent to one another. In some cases the fruit will ripen and the seeds will be dispersed during a wet period a few months later. Similar coordination of flowering is observed in some evergreen trees.

Evergreen Species

The evergreen tree *Fagraea fragrans* (Loganiaceae) flowered heavily in May about four months after the end of the wet season in Singapore, when a week of dry weather followed by rain seemed to initiate flower buds regularly each year, although some slight irregular flowering occurred in October and November (Holttum, 1940). In *Saraca taipingensis* (Leguminosae) wet weather seemed to stimulate leaf change (c.f. dry weather in *Hevea*) but flowering was independent of leaf change and was often twice a year about one month after the beginning of dry weather.

Fungi

The "toadstool" seasons in Singapore and south Johore are March to May and August or September (rarely October) to October or early December. Corner (1935) suggested that the cessation of mycelial growth during the dry spell triggered the development of fructifications; rain was not the trigger, but necessary to revive growth of the mycelium including the emergence of the fruitifications.

Effects on Animals

Plant life as the primary producer affects animal life. The phenological behavior of plants may affect animal activity by the availability of preferred forms of food, e.g. young foliage, nectar in flowers, and fruit. Ellis, Carlisle, and Osborne (1965) found that a diet of senescent vegetation delayed sexual maturity in the desert locust. Senescent leaves are deficient in gibberellins and a supplement with GA restored the rate of maturation to that of insects feeding on green leaves.

Conclusions

Stimuli:

1a. Photoperiodic, including meteorological reinforcement of the astronomical photoperiod. *Oryza, Euphorbia, Coffea.*

1b. Photoperiodic induction of senescence and susceptibility to other stimuli in deciduous trees. *Hevea*, etc.

2. Release of water stress. *Coffea.*

3. Cooling, sudden or prolonged. *Bromheadia, Clerondendron, Coffea, Dendrobium, Epiphyllum, Murraya, Palaquium, Phalaenopsis, Pterocarpus, Randia, Saccolabium, Thrixspermum* and *Zephyranthes.*

4. Accumulation of assimilates and associated biochemical conditions following high insolation. Speculatively in the Dipterocarpaceae.

5. Water stress, during opposed phases of the pluvial and solar (warm drying) cycles. *Hevea, Elateriospermum*, many deciduous trees, some evergreen trees, *Fagraea* and *Saraca*, toadstool fungi.

Different stimuli may operate at different stages in the same plant, e.g., flower initiation by short days in *Coffea* and the triggering of anthesis by the 'storm' syndrome. The accumulation of assimilates may determine the long term variation in the flowering and fruiting of Dipterocarpaceae but the more immediate trigger may be water stress as appears so in many other trees. The ageing processes of the leaves provide an internal mechanism to co-ordinate the responses to external stimuli.

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