

CLIMATIC A SEASONALITY, PHENOLOGICAL DIFFERENTIATION AND SPECIATION IN TREES

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Nearly everywhere in the world, plant phenology is tightly linked with climatic seasonality. When all the individuals of a species flower at the same time each year, they are genetically linked to each other by cross-pollination. Phenological conformity maintains the genetic integrity that defines a species. Where the climate allows individuals of a species to flower at different times, individuals and subpopulations of a species may get reproductively isolated from each other. Since reproductive isolation is the essential first step for the evolution of a new species from a pre-existing one, it may be argued that wherever the climate is least effective in regimenting phenological behaviour, there would be maximum opportunities for phenological differentiation and reproductive isolation, and maximum opportunities for sympatric speciation. Data from the Malay Peninsula is presented to support this hypothesis. The Malay Peninsula has an exceptionally large number of species in relation to its land area, a wider range of well-documented phenological expressions than any other region of the world, and what appears to be the least seasonal of all climates.

Keywords: Humid tropics, aseasonality, sympatric speciation, reproductive biology, evolution.

INTRODUCTION

The life of a tree is a succession of events such as leaf-production, flowering, fruiting, and leaf-fall, repeated in cycles. Phenology is the study of these cycles, usually in relation to climate and crop production. The relationship between phenology and speciation has received little or no attention. Nearly everywhere in the world, the climate is seasonal, and the phases of plant growth and reproduction are tightly linked to the climatic seasons. Most importantly, when the individuals of a species flower synchronously, they are genetically linked to each other by cross-pollination and this maintains the genetic integrity that defines a species. New species can come into existence only when individuals or subpopulations of an existing species can somehow get reproductively disconnected or isolated from their peers and are then free to evolve independently. This study examines the hypothesis that a non-seasonal climate would allow for phenological diversity to arise within a species and create opportunities for sympatric speciation.

The best place to test this hypothesis would be in the tropics, which collectively contain over 50% of the world's species (Olson & Dinerstein 2002) although covering less than 10% of the global land area. There is a gradient in biodiversity, from minimum in the polar regions to maximum in the equatorial belt. The term Latitudinal Diversity Gradient (LDG) has been applied to this gradient (Brown 2014). The simplest assumption is that warm climates promote speciation. However, although India, Myanmar, and the Malay Peninsula all have warm climates, it was already known early in the 20th Century (Foxworthy 1927) that the number of species of trees in the small area of the Malay Peninsula was equal to the total for the vast area of India and Myanmar combined. Hence factors other than temperature must be involved as drivers of speciation. Most significantly, the Malay Peninsula has a large number of genera containing a multiplicity of sympatric species (Table 1).

Table 1 The most species-rich genera in the Malay Peninsula

Genus	Family	No. of species in Malay Peninsula
<i>Syzygium</i> (listed as <i>Eugenia</i>)	Myrtaceae	193
<i>Ficus</i>	Moraceae	101
<i>Ardisia</i>	Myrsinaceae	72
<i>Diospyros</i>	Ebenaceae	70
<i>Shorea</i>	Dipterocarpaceae	60
<i>Psychotria</i>	Rubiaceae	55
<i>Litsea</i>	Lauraceae	54
<i>Lasianthus</i>	Rubiaceae	54
<i>Garcinia</i>	Guttiferae	49
<i>Calophyllum</i>	Guttiferae	45
<i>Aglaiia</i>	Meliaceae	44
<i>Lithocarpus</i>	Fagaceae	38
<i>Tarenna</i>	Rubiaceae	37
<i>Hopea</i>	Dipterocarpaceae	32
<i>Dipterocarpus</i>	Dipterocarpaceae	31
<i>Cleistanthus</i>	Euphorbiaceae	29
<i>Polyalthia</i>	Annonaceae	28
<i>Memecylon</i>	Melastomataceae	28
<i>Elaeocarpus</i>	Elaeocarpaceae	27
<i>Mallotus</i>	Euphorbiaceae	27
<i>Macaranga</i>	Euphorbiaceae	27
<i>Urophyllum</i>	Rubiaceae	26
<i>Aporosa</i>	Euphorbiaceae	25
<i>Schefflera</i>	Araliaceae	24
<i>Glochidion</i>	Euphorbiaceae	24
<i>Vatica</i>	Dipterocarpaceae	23
<i>Sterculia</i>	Sterculiaceae	22
<i>Palaquium</i>	Sapotaceae	22
<i>Phyllanthus</i>	Euphorbiaceae	22
<i>Symplocos</i>	Symplocaceae	21
<i>Cinnamomum</i>	Lauraceae	21
<i>Xanthophyllum</i>	Polygalaceae	21
<i>Baccaurea</i>	Euphorbiaceae	20

Based on Whitmore & Ng (1972–1989) for non-dipterocarps and Symington (2004) for dipterocarps

Regional comparisons of species richness—the Regional Species Intensity (RSI) Index

The comparison of species richness between regions is complicated by differences in the size of the regions compared. For better comparison, differences in size should be evened out, and the regions themselves should be defined by natural rather than political boundaries. The only part

of the world that has been divided consistently into natural biogeographical regions is the Malay Archipelago. This archipelago is wholly situated within the tropics and is divided between six countries: Brunei, Indonesia, Malaysia, Philippines, Singapore, and Timor-Leste, but biologists have consistently ignored national boundaries and recognized nine well-defined biogeographical regions separated by open seas.

In order of size, these are the Moluccas, the Lesser Sunda Islands, the Malay Peninsula, Java, Sulawesi, Philippines, Sumatra, Borneo, and New Guinea.

Many monographs of plant families have been completed under the Flora Malesiana Programme that covers the Malay Archipelago. Each monograph deals with a whole family and covers all nine regions of the archipelago. Each family is by a single author or a small number of co-authors, hence each treatment is internally consistent. We have devised a measure, called the Regional Species Intensity (RSI) index (Ng et al. 2022), by dividing the number of species in each targeted family of plants by the land area in thousands of km² of its biogeographical region. This eliminates the bias of land area. The RSI may then be used as a measure of the intensity of speciation in each region.

Table 2 shows that in the family Dipterocarpaceae, the region with the largest number of species is Borneo, with 267 species compared with 158 species in the Malay Peninsula. However, the RSI for Dipterocarpaceae in the Malay Peninsula is 1.18, far exceeding the RSI of 0.36 for Borneo. The high RSI for Dipterocarpaceae in the Malay Peninsula is paralleled by similarly high RSI indices for many other families e.g. Apocynaceae, Moraceae, Nepenthaceae, Arecaceae, Zingiberaceae, Gesneriaceae and Melastomataceae (Tables 2 & 3). Where the Malay Peninsula does not come out on top, it is second, as in Orchidaceae, and third

as in Moraceae. This implies that the conditions for speciation of plants have been much more favourable in the Malay Peninsula than in other regions of the Archipelago although all share a tropical climate.

Niche differentiation and niche dynamics as drivers of speciation

In an effort to explain the high Regional Species Intensity of the Malay Peninsula, Ng et al. (2022) examined niche dynamics in the Peninsula. Dipterocarp forests are taller than forests in tropical Africa and tropical America by about 10 m and the greater height provides more opportunities for niche proliferation. Niche proliferation is also promoted by the development of crown-shyness that breaks up the canopy into innumerable discrete islands of foliage. Tall trees and crown shyness may have influenced the evolution of gliding animals and this would explain why the biodiversity of gliding animals is much greater in the dipterocarp forests of tropical Asia than in the forests of tropical Africa and tropical America. Furthermore, the trees in the Peninsula appear to have shorter life spans than trees of other climates, thereby contributing to higher rates of niche turnover. Also, the phenomenon of mass flowering followed by mast fruiting, unique to the Peninsula and north Borneo, produces extremes between periods of plenty and scarcity, causing niches to drastically expand and contract

Table 2 Species distribution of Dipterocarpaceae, Apocynaceae and Nepenthaceae in the Malay Archipelago

Region	Land area in 1000 km ²	Dipterocarpaceae		Apocynaceae		Moraceae (<i>Ficus & Artocarpus</i>)		Nepenthaceae	
		No. of species	RSI	No. of species	RSI	No. of species	RSI	No. of species	RSI
Moluccas	55	6	0.11	45	0.82	86	1.56	3	0.05
Lesser Sunda Islands	92	3	0.03	29	0.32	38	0.41	0	0.00
Malay Peninsula	133	158	1.18	110	0.83	110	0.83	11	0.08
Java	149	10	0.07	49	0.33	79	0.53	2	0.01
Sulawesi	193	7	0.04	50	0.26	83	0.43	8	0.02
Philippines	300	50	0.17	73	0.24	98	0.33	12	0.04
Sumatra	473	106	0.22	78	0.17	106	0.22	32	0.07
Borneo	748	267	0.36	101	0.14	160	0.21	35	0.05
New Guinea	786	15	0.02	102	0.13	144	0.15	11	0.01

Based on Flora Malesiana revisions by Ashton 1982, Middleton 2007, Berg & Corner 2005, Berg *et al.* 2006, Cheek & Jebb 2001; RSI = Regional Species Intensity Index

Table 3 Species distribution of Arecaceae, Zingiberaceae, Orchidaceae and Melastomataceae by biogeographical region in the Malay Archipelago

Region	Land area in 1000 km ²	Arecaceae		Zingiberaceae		Orchidaceae		Gesneriaceae		Melastomataceae	
		No. of species	RSI	No. of species	RSI	No. of species	RSI	No. of species	RSI	No. of species	RSI
Moluccas	55	49	0.9	23	0.4	429	7.8	21	0.4	40	0.7
Lesser Sunda Islands	92	18	0.2	23	0.3	299	3.3	23	0.3	10	0.1
Malay Peninsula	133	239	1.8	220	1.7	987	7.4	214	1.6	176	1.3
Java	149	50	0.3	70	0.5	776	5.2	62	0.4	69	0.5
Sulawesi	193	66	0.3	79	0.4	693	3.6	75	0.4	37	0.2
Philippines	300	130	0.4	112	0.4	1196	4.0	178	0.6	182	0.6
Sumatra	473	168	0.4	101	0.2	1188	2.5	127	0.3	120	0.3
Borneo	748	296	0.4	257	0.3	1707	2.3	305	0.4	314	0.4
New Guinea	786	231	0.3	195	0.3	2800	3.6	203	0.3	202	0.3

Based on Plants of the World Online (2021) by the Royal Botanic Gardens, Kew; RSI = Regional Species Intensity Index

alternately. Niche proliferation and high niche turnover rates would support the evolution of species to occupy those niches but would not explain how reproductive isolation can develop. Without reproductive isolation, speciation cannot proceed, no matter how many different niches are available.

Phenological differentiation as the cause of reproductive isolation

Nearly everywhere in the world, if a tree is observed flowering at a particular time of the year, that tree, and all other individuals of its species in the same area may be expected to flower at that same time every year. However, in the Malay Peninsula, a single observation of a tree in flower cannot be used to predict when that tree will flower next. Many observations are needed to confirm a pattern for the individual and for its species. Species and individuals may flower continuously, or once a year, or twice a year, or at unpredictable intervals of two or more years, or sporadically at any time of the year. Even after many observations, we may still be unable to predict when a particular tree will flower next time.

Newstrom et al. (1994), studied the phenology of trees in a lowland tropical rain forest in Costa Rica, recognized four patterns of flowering:

continual, sub-annual, annual and supra-annual, and mooted the idea of phenological differentiation being a driver for speciation, but they did not develop the idea further.

The climate of the Malay Peninsula

The nine biogeographic regions of the Malay Archipelago lie between the Tropics of Cancer and Capricorn, and have consistently warm temperatures throughout the year. Maritime influences pervade and prevent the development of continental temperature extremes. In the Malay Peninsula, the difference in day length between mid-summer and mid-winter is 9 minutes at the southern end (Singapore) and 38 minutes in Gerik close to the northern end. The maximum temperature recorded is 39 °C and the minimum is 15 °C. The annual rainfall varies greatly from place to place, depending on local topographic peculiarities (Wyatt-Smith 1995), between 1,651 mm at Jelebu and 4,216.4 mm at Taiping. However, the Malay Peninsula does not experience drought conditions because there is rain every month and it is unusual for any period to be without rain for as long as 10 consecutive days. In every study of phenology in the Malay Peninsula the authors have tried to link flowering with periods without rain and all have failed to find any connection. The rainless periods are

too short to have effect on plant behaviour. The climate of the Malay Peninsula qualifies as the most aseasonal in the archipelago and possibly in the world. East Java and the Lesser Sunda Islands have long droughts that divide the year into dry and wet seasons while other parts of the Archipelago lie between these two extremes.

Continuous flowering

Continuous flowering is the habit of many species of open habitats. Land that has been cleared of forests and then abandoned is colonized by pioneer species, and many pioneer species flower and fruit continuously. They include woody species such as *Adinandra dumosa*, *Dillenia suffruticosa*, *Leucaena leucocephala*, *Melastoma malabathricum*, *Muntingia calabura*, *Ploiarium alternifolium*, and *Trema orientalis*. Many fruit trees also flower and fruit continuously. These include the guava (*Psidium guajava*), jackfruit (*Artocarpus heterophyllus*), papaya (*Carica papaya*), soursop (*Annona muricata*), and starfruit (*Averrhoa carambola*). The total number of ever-flowering species, including weedy herbs that germinate, grow, flower and seed at all times of the year, would run into hundreds. To ever-flowering species, there are no seasons. By this indicator, the climate of the Peninsula is aseasonal.

Annual flowering

In practically all other parts of the world, annual flowering is the normal behaviour for plants, but in the Malay Peninsula, strict annual flowering is unknown. The closest documented example is tembusu, *Cyrtophyllum fragrans* (*Fagraea fragrans*) which Holttum (1940) observed to flower in May every year in Singapore. However, he added, “There tends to be a small flowering in about October–November, but this is irregular, and a few flowers may occur on isolated trees also at other times...”

Table 4 lists the flowering specimens of tembusu in the herbarium of the Forest Research Institute Malaysia, arranged by month of collection, and their locations. Taking the Peninsula as a whole, there are over 20 flowering records. From the records, April–May–June is when flowering is most frequently observed, with the peak in May. But flowering also occurs in other months. Hence even in the best example of an annual flowering tree, we find

individuals flowering at other months of the year. Hence Holttum’s observations in Singapore are confirmed by herbarium records from the rest of the Malay Peninsula.

Flowering and fruiting twice a year

The most famous fruits of the Malay Peninsula are four indigenous species that fruit twice a year, at mid-year and at year’s-end. These are the durian (*Durio zebithinus*), mangosteen (*Garcinia mangostana*), langsung (*Lansium domesticum*) and rambutan (*Nephelium lappaceum*). The two fruiting periods, in mid-year (June–August) and year-end (November–January), have been described by Milsum (1919), Corner (1940), Molesworth-Allen (1967) and Sahadevan (1987). In all four species, the time from flowering (anthesis) to fruit-ripening is 3–4 months. Anthesis occurs in March–May and again in August–October. Milsum observed that the mid-year crop is a major crop and the year-end crop is minor. Corner, Molesworth-Allen, and Sahadevan did not make such a distinction. My own experience is that the mid-year crop is often but not always the heavier crop.

Where these species have been planted in other parts of the tropics, even in nearby Indonesia (Ochse 1931) and the Philippines (Coronel 1983), they produce only one crop a year (Table 5). Elsewhere, the only other mention of two reproductive periods a year is for Vanuatu (New Hebrides) (Richards 1952), which has an ‘exceptionally unvarying climate’ with two main flowering periods, one from September to January and the other in May–June. The phenomenon of two reproductive periods a year applies collectively to the species. There have been no studies to track the behaviour of individuals through extended periods of time. The occurrence of two crops every year indicates seasonality but it is not the normal kind of seasonality that produces one crop a year. Furthermore, the timing of the two crops has become increasingly variable. For example, durian, mangosteen and langsung started to appear in markets in Kuala Lumpur and parts of Johore in October 2022, extending the year-end November–January period of fruiting by one month. This may have been the result of growers deliberately selecting trees to prolong the crop production periods. The climate allows for this. Eventually, durians may become available throughout the year.

Table 4 Phenology of *Cyrtophyllum fragrans* based on herbarium specimens in the Forest Research Institute Malaysia

Month and year collected in flower	Specimen reference	Location of tree
January	-	-
February	-	-
March	-	-
April 1927	KEP 19601	Negri Sembilan
April 1927	KEP 19851	Negri Sembilan
April 1965	KEP 99076	Kepong, Selangor
Apr 1981	FRI 29649	Kepong, Selangor
May 1923	KEP 7980	Kuala Lumpur
May 1927	KEP 18856	Seremban, Negri Sembilan
May 1929	KEP 15735	Kuantan, Pahang
May 1934	KEP 15649	Kuantan, Pahang
May 1949	KEP 64867	Kepong, Selangor
May 1949	KEP 64868	Kepong, Selangor
May 1967	FRI 3714	Kuantan, Pahang
May 1968	Ogata 10344	Penang
May 1976	FRI 23494	Kepong, Selangor
June 1916	Ridley 63	Negri Sembilan
June 1925	Mohd Nur 3414	Singapore
June 1980	FRI 25414	Kepong, Selangor
July 1931	KEP 26996	Kemaman, Terengganu
August 1922	KEP 7425	Kuala Lumpur
September 1928	KEP 15217	Kuala Lumpur
October 2010	KL 5745	Kedah
October 2012	LYW 522	Singapore
November	-	-
December 1925	KEP 9037	Kedah
December 1930	KEP 23732	Bangi, Selangor

Mass flowering and sporadic flowering

The forests of the Malay Peninsula contain about 2830 species of trees belonging to about 100 families of plants (Ng et al. 1990). One family, the Dipterocarpaceae, is represented by 155 species and it dominates the forests from sea level up to about 1300 m elevation by frequency and by the size of its trees. Symington (1943) estimated that in the lowland forests, dipterocarps account for 30% of trees by frequency and 55.5% by timber volume.

The Malayan Forestry Department, established in 1901, needed to understand the dynamics of natural regeneration of the forests, which was unlike anything that the

colonial forest officers had experienced in Europe and North America and even in India. It was recognized quickly that there were years of abundant fruiting, interspersed with years of sparse fruiting. New words had to be made up to describe phenomena that nobody yet understood. The year 1904 was described as a 'good fruiting year' for dipterocarps (Wyatt-Smith 1995). Next was 1916, which was described as an 'unprecedented seed year'. The years of abundance were also referred to 'general' and 'gregarious' flowering years. The terms 'mass flowering' and 'mast fruiting' are now preferred. Mast is a word originally applied to the unusually heavy fruiting events that occur at non-annual intervals in England.

Table 5 Fruiting times of durian, mangosteen, langsung and rambutan

Species	Origin	Malay Peninsula	Indonesia (Java)	Philippines	Brazil
		Milsum (1919), Corner (1940), Molesworth-Allen (1967), Sahadevan (1987).	Ochse (1931)	Coronel (1983)	Lorenzi <i>et al</i> (2006)
<i>Durio zebithinus</i> (durian)	Malay Peninsula	Two crops: * Mar–May fr Jun–Aug * Aug–Oct fr Nov–Jan	One crop: * Jun–Sep fr Oct–Feb	One crop: * Apr–Jun fr Aug–Nov	One crop* * Dec–Jan
<i>Garcinia mangostana</i> (mangosteen)	Malay Peninsula	Two crops: * Mar–May fr Jun–Aug. * Aug–Oct fr Nov–Jan	One crop: * Jul–Oct fr Nov–Mar	One crop: * Apr fr Jun–Dec	One crop* * May–Aug. fr Nov–Feb
<i>Lansium domesticum</i> (langsar)	Malay Peninsula	Two crops: * Mar–May fr Jun–Aug * Aug–Oct fr Nov–Jan	One crop: * Dec–Jan fr Mar–Apr	One crop: (Luzon) *Apr–Jun fr Aug–Oct	–
<i>Nephelium lappaceum</i> (rambutan)	Malay Peninsula	Two crops: * Mar–May fr Jun–Aug * Aug–Oct fr Nov–Jan	One crop: * Jul–Sep fr Nov–Feb	One crop: * Mar–Jun fr Aug–Oct	One crop: * Dec–Feb

* = flowering, fr = fruiting

F.W. Foxworthy, who was appointed head of forestry research in 1918, thought that the reproductive behaviour of the forests could be clarified without too much effort. He made it a point to comment on phenology in his annual reports (Ng 2018), based on his own observations and on information provided by forest officers from the various forest districts in the Peninsula. His notes are summarised in Table 6 to illustrate how he failed to make sense of phenology in the Malay Peninsula and had to give up.

He concluded (Foxworthy 1927) that “a definite season for flower and fruit is lacking for many, or most, forms”. In his 1933 Annual Report, his phenology report ended with the following passage, “It is doubtful whether general

records of fruiting are worth continuing, based as they are on casual observations. A better idea of the periodicity of the different species could probably be obtained by maintaining records of regular observations in conveniently situated areas set aside for the purpose”. Foxworthy experienced three mass flowering events, spaced three to six years apart but he did not pay attention to the months in which these events occurred.

Burgess (1972) examined Forest Department reports of dipterocarp flowering, totalling 1,482 reports, between 1960 and 1970 and found a clear peak of reports in April–May (Table 7). Mass flowering occurred at intervals of up to 6 years, but when it occurred, it would be in March–July,

Table 6 Phenological observations by Foxworthy from 1918 to 1933

Year	Phenological observation	Interval from previous mass flowering event
1918	It would appear that dipterocarps flower and fruit more frequently and more regularly than had been supposed.	
1919	There did not seem to be anything like so much flower as there had been at the same time in 1918. Sporadic individuals of certain kinds of trees are often found in flower or fruit when there is not a general flowering season. It will take a good many observations to determine what the normal flowering seasons are.	
1920	The latter part of the year saw exceedingly heavy fruiting of some of the dipterocarps.	4 years from the 'unprecedented' seed year of 1916
1921	(A list of species observed flowering was provided, without comment)	
1922	The year does not seem to have been a good flowering year.	
1923	The year was not phenomenal as regards the amount of fruit.	
1924	(A list of species observed flowering was provided, without comment)	
1925	The year was not a particularly good year for flower and fruit and we received only a limited number of observations.	
1926	The year was a good one for seed production	6 years
1927	The year was not at all a favourable year for the production of seed though sporadic flowering and fruiting of a large number of species occurred throughout the country	
1928	It has proved to be a poor year for flowering and fruiting in most districts. There has, of course, been sporadic flowering and fruiting in most or all districts.	
1929	No report	
1930	The year seems to have been a particularly good year for flowering and fruiting.	3 years
1931	The year was not a conspicuously good one for flowering and fruiting.	
1932	Reports of fruiting of timber trees were meagre.	
1933	Reports from the districts indicate that there was no general fruiting of commercial forms.	

Table 7 Distribution of flowering reports of dipterocarps by month

Month	Percentage of reports on flowering
January	2
February	4
March	11
April	20
May	31
June	16
July	10
August	2
September	1
October	1
November	1
December	1
Total	100

Based on a total of 1482 reports between 1960 and 1970 (Burgess 1972)

peaking in May. In other months, flowering would be sparse and ‘sporadic’.

The only study on phenology in pristine primary natural forest is a study by Medway (1972) in a Hill Dipterocarp Forest at 515 m above sea level in Ulu Gombak in the state of Selangor. Observations were carried fortnightly from a platform constructed in the crown of a tall dipterocarp tree (*Anisoptera laevis*) at 43 meters above the ground overlooking a confluence of two streams, affording a view of two flanks of a steep gully. 61 trees belonging to 45 species, 18 families, were kept under observation between

July 1963 and July 1969—a period of 6½ years. The Dipterocarpaceae was represented by 18 trees, in four genera. Table 8 shows clearly that 1963 and 1968 were years of mast fruiting.

Medway’s data on flowering (Table 9) placed the period of mass flowering in 1968 in April–July. For 1963 there was no data until July when the tail end of mass flowering was recorded. Sporadic flowering could occur in any month.

Medway also noted the months when new leaves were produced (Table 10). In the Malay Peninsula trees (with very rare exceptions) have no deciduous period. Instead, there are leaf-

Table 8 Fruiting, expressed as a percentage of trees in a Hill Dipterocarp Forest

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1963	-	-	-	-	-	-	43	50	57	55	34	19
1964	5	3	7	7	12	14	14	21	19	16	10	12
1965	12	9	9	14	21	24	19	24	21	16	16	7
1966	7	5	3	10	14	12	17	16	12	3	7	9
1967	5	4	4	7	14	14	14	23	27	23	9	2
1968	2	4	7	13	19	39	58	55	47	41	3	8
1969	2	2	6	15	17	15	13	-	-	-	-	-

Table 9 Flowering, expressed as a percentage of trees in a Hill Dipterocarp Forest

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1963	-	-	-	-	-	-	24	12	7	0	0	0
1964	2	9	12	3	9	7	7	2	3	3	2	2
1965	2	14	16	12	2	3	7	0	2	0	3	0
1966	0	7	10	12	16	17	12	2	7	7	2	2
1967	0	4	7	11	9	10	16	7	0	0	2	0
1968	0	11	11	22	30	35	24	2	2	4	6	0
1969	0	4	15	4	4	6	4	-	-	-	-	-

Table 10 Flushing expressed as a percentage of trees in a Hill Dipterocarp Forest

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1963	-	-	-	-	-	-	7	2	12	24	12	12
1964	7	3	24	3	12	17	5	7	5	16	2	12
1965	12	16	38	20	17	14	10	10	5	10	12	14
1966	5	10	28	26	16	12	12	7	10	10	11	21
1967	5	4	11	29	21	18	14	11	5	7	17	11
1968	15	17	33	17	13	6	6	4	9	6	13	13
1969	8	6	23	17	29	10	12	-	-	-	-	-

exchange episodes in which new flushes of leaves appear and old leaves are shed simultaneously thereby eliminating the deciduous period. Inflorescences would be produced with the new flushes, but often, inflorescences fail to develop. Hence flushing alone is more frequent than flushing accompanied by flowering.

After Medway, the next detailed study of phenology was by the present author (Ng 1977) who kept under monthly observation 87 planted trees belonging to 8 genera of dipterocarps in the Dipterocarp Arboretum of the Forest Research Institute Malaysia from January 1972 to August 1976. Ng’s data is summarised in Table 11. In this record, a flowering episode is only recorded for the first month in which the flowering is observed. Hence the totals in the last column are the total of trees that flowered in the year.

Year 1976 was a mass flowering year with 79 trees or 91% of the all-dipterocarp population flowering. In other years, the percentage of trees flowering was 7% to 26%. The visual impact of mass flowering is much greater than what the percentages suggest because in mass flowering, the flowering is concentrated in a few months while sporadic flowering is dispersed through the whole year.

I recorded flowering in March–April, Medway in April–July and Burgess in March–July. I recorded the time when inflorescences first became visible. Other observers would have recorded the months when flowers were visible, which would be one month after the initiation of inflorescences and continuing until the inflorescences were exhausted, in July. Medway’s placement of leaf-flushing in March–April actually indicates that the month of flower initiation is March–April because the initiation of leaf flushes would have coincided with the initiation of inflorescences.

Outside of the Malay Peninsula, mass flowering and mast fruiting have been described in Sabah (North Borneo) (Wood 1956), who observed the

event in 1955. He wrote, “...the 1955 dipterocarp flowering in North Borneo was a magnificent spectacle which as a botanist I felt privileged to witness.” He noted that both dipterocarps and non-dipterocarps were involved, that flowering began in early April and the fruits of most species fell in September and October.

The stimulus for mass flowering is unknown but drought or low rainfall has been discounted in every study. It is significant that trees on river banks and swamp forests, that do not experience water stress, follow the mass flowering pattern of areas distant from water bodies.

Other phenological cycles: *Peltophorum pterocarpum* and *Samanea saman*

Two trees of *Peltophorum pterocarpum*, of the same size and located next to each other in the Forest Research Institute Malaysia were kept under phenological observation for seven years: 1972 to 1979 (Ng 1980). A cycle starts with leaf exchange, followed by terminal flowering of the new shoots, followed by fruit maturation. The cycle ends with the ripening of fruits and the shedding of leaves, coinciding with the flushing of new leaves of the next cycle. One tree operated on a cycle of 6 months and the other on a cycle of 9 months. It so happens that Holttum (1930) kept three trees of this species under observation in the Botanic Gardens Singapore from 1928 to 1937 and found that two operated on a cycle of 6 months while the third operated on a cycle of 6.8 (nearly 7) months. As a result of variation in the length of phenological cycle, trees in an avenue of *Peltophorum* trees never flower at the same time.

Samanea saman is a large spreading tree often planted to provide shade in towns. I kept a big tree at the Forest Research Institute Malaysia under observation from 1973 to 1980. *Samanea saman* is native to Central America where it follows a strict annual cycle and is deciduous during the dry season that lasts several months.

Table 11 Flowering of trees in the Dipterocarp Arboretum of FRIM

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1972	0	0	3	1	1	1	0	0	0	2	4	0	12
1973	0	0	5	11	1	2	0	0	0	2	0	1	22
1974	0	1	6	7	4	3	0	0	0	0	1	1	23
1975	0	1	2	1	0	1	0	0	0	0	0	1	6
1976	1	8	24	45	1	0	0	0	-	-	-	-	79

The tree is never deciduous in Malaysia. Instead, it goes through periodic leaf change during which it sheds all its leaves and simultaneously flushes new leaves. My tree went through leaf change at six-month intervals, in February and in August.

Unpredictable cycles: the case of the avocado (*Persea Americana*)

Avocados have been grown in the Malay Peninsula for about 100 years in private gardens. The plants were raised from seeds and found to be highly variable in phenology. Table 12 shows the behaviour of two genetically identical trees. Tree B was cloned from Tree A and the two trees were planted about 10 m apart on a roadside. Tree A was destroyed by roadworks after the flowering of July 2020 while Tree B started flowering in December 2019. The time of overlap was small but enough to show that trees of the same clone grown close to each other can behave differently. They flowered at different times and the interval between flowering episodes could vary between 3 and 22 months.

The meaning of aseasonality

There have been periods in geological time (Morley 1998) when the climate of the Malay Peninsula was seasonal. Tropical rain forests and seasonally dry forests have alternated with each other and trees would have shifted in behaviour to fit the prevailing climate. The shift between leaf exchange and the deciduous habit is relatively simple, as shown in the example of *Samanea saman*, which is deciduous in the seasonally dry forests of Costa Rica but leaf-exchanging in the Malay Peninsula. The tree that I observed had a six-month phenological cycle and could fit two cycles neatly into one year, with leaf-exchange events in February and August.

In the case of species with phenological cycles different from six months or twelve months, leaf-exchange under aseasonal conditions would occur in a different month each time. If leaf-exchange is only intermittently accompanied by flowering, flowering in an aseasonal climate would occur at supra-annual intervals.

The shift between continuous flowering and seasonal flowering can be explained by

Table 12 Flowering of two avocado trees in Kuala Lumpur

Tree A		Tree B	
Month and year of flowering start	Interval in months from previous event	Month and year of flowering start	Interval in months from previous event
2001 Mar	–		
2002 Mar	12		
2002 Dec	9		
2004 Mar	15		
2005 Nov	20		
2007 Mar	16		
2007 Sep	6		
2009 Jan	16		
2010 Jan	12		
2011 Jan	12		
2012 Nov	22		
2014 Nov	24		
2016 Feb	15		
2018 Feb	24		
2018 Sep	7	2019 Dec	–
2020 Jul	22	2020 Jun	6
		2020 Oct	4
		2021 Jan	3
		2021 Dec	11

loss synchronisation in bud development in the crown. This can be seen clearly in species of frangipanni, *Plumeria*, which flower once a year in a seasonal climate but continuously in the Malay Peninsula; in a seasonal climate, bud development is synchronized across the entire crown and each shoot flowers after producing a certain number of leaves, but in the Malay Peninsula, bud development is totally unsynchronised, so the crown consists of shoots in different stages of growth and flowering.

An aseasonal climate would allow differences in leaf longevity and nutrient status, and localised events like sudden drops in temperature of a few degrees during the onset of a thunderstorm, to affect phenological events.

The important conclusion is that aseasonality allows for maximum phenological diversity. The wealth of tree species in the tropics may in general be because the various parts of the tropics have experienced periods of climatic aseasonality during which they became hotspots for species proliferation.

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