

## Phenology of seasonally dry tropical forest

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There exists considerable diversity in leaf flushing, leaf-fall, flowering, fruiting and fruit-fall among plant species in a seasonally dry tropical forest. Leaf-fall is initiated with the onset of the post-monsoon, low-temperature dry period, and leaf flushing begins with the rise in temperature and peaks in the hottest and driest period (May) of the year renovating the canopy before the onset of the monsoon. Although flowering is staggered, its peak coincides with the peak in leafing. The fruiting phenology follows closely the flowering phenology. Fruit-fall culminates before or just at the beginning of the monsoon season and thus ensures availability of sufficient moisture to seeds for germination and seedling establishment. The phenological clock of the seasonally dry tropical forest appears to be set during the interphase of winter and summer ensuring full advantage of the short rainy season that follows.

INFORMATION on phenology (derived from the Greek word *Phaino* meaning to show or to appear) is important for the study of plant-animal interactions which affect pollination and dispersal, and are important for plant reproduction<sup>1</sup>. The periodicity in phenological events reflects the temporal distribution of various kinds of available food resources for animals. Selected phenological events can be useful as indicators on which major land management practices, productivity

studies, and ecosystem analysis can be keyed<sup>2,3</sup>. Phenology of the tropical dry forest is not well understood, although water stress is most frequently cited as a primary factor responsible for the timing of phenological events<sup>4</sup>. The importance of biotic factors, particularly seasonality in populations of pollinators, seed dispersal agents, predators, and competitors, in the evolution of tropical phenological patterns has been suggested in several studies<sup>5</sup>. Our studies indicate that the phenological clock of the seasonally dry forest is reset each year during the dry warm period of the annual cycle and that there is a considerable diversity in the timing and duration of phenophases.

The study area is located on Vindhyan plateau, in Sonbhadra district of Uttar Pradesh, India between 24° 12' 41" to 24° 26' 36" N lat. and 82° 52' 48" to 83° 6' 36" E long. The elevation above mean sea level ranges between 315 to 485 m. The climatic description is based on temperature and rainfall data collected for

1981–1988 by the State Irrigation Department at Renukoot (Figure 1a). Mean maximum monthly temperature varies from 20°C in January to 39°C in May, and the mean minimum from 14°C in January to 31°C in June. The year is divisible into three seasons: summer (April to mid June); winter (November to February); and rainy (mid June to September). October and March constitute the transition months, between the rainy season and winter, and between winter and summer seasons, respectively. Average monthly rainfall ranges from 3 mm (November) to 319 mm (August). Annual rainfall averages 1145 mm. About 85 per cent of the annual rainfall occurs during the rainy season from the S. W. monsoon. During the study period (April 1987–March 1988) the rainfall was 1678 mm, the mean maximum monthly temperature varied from 20°C in January to 46°C in June, and the mean minimum monthly temperature from 12°C in January to 31°C in May. The soils are nutrient-poor, residual ultisols,

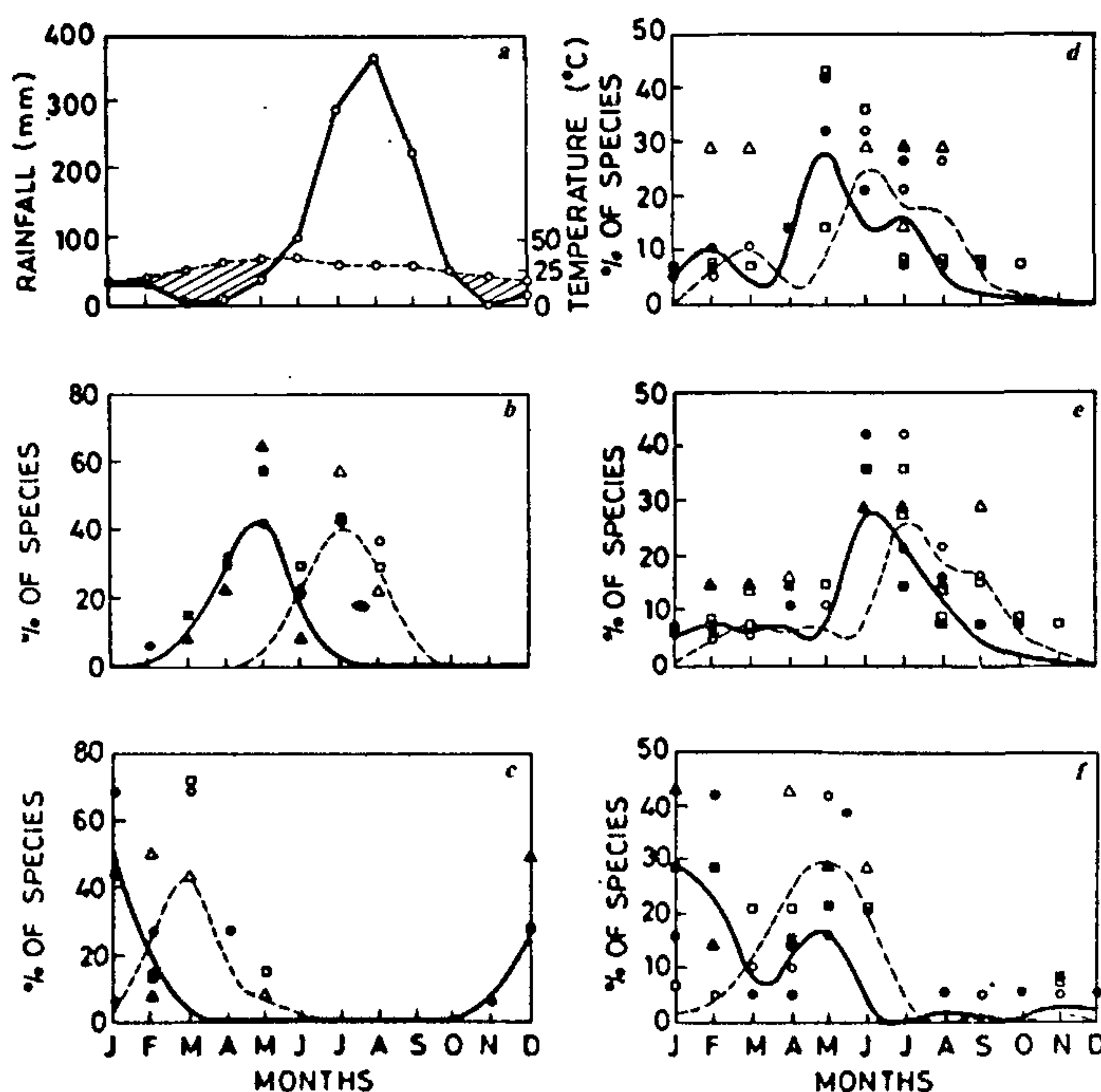


Figure 1. *a*, Ombrothermic diagram for the study area, solid curve—rainfall, broken curve—mean temperature; hatched area shows xeric conditions; *b*, initiation and completion of leafing; *c*, initiation and completion of leaf fall; *d*, initiation and completion of flowering; *e*, initiation and completion of fruiting, and *f*, initiation and completion of fruit-fall. Data for site I are represented by circles, for site II by triangles and for site III by squares. Solid symbols are for initiation and open symbols for completion of phenological events. The smooth curves (solid, for initiation and broken, for completion of various phenological activities) are fitted by using Harvard Graphics<sup>®</sup>.



## RESEARCH COMMUNICATIONS

sandy loam in texture and reddish to dark gray in colour.

Three sites were selected. Site I comprised a north-facing slope, was comparatively moist due to the presence of a stream and the forest was dense (stems  $\geq 30$  cm circumference at breast height = 2210/ha). Sites II and III were located on a plateau, were drier, and tree densities were 950 and 760 stems/ha, respectively. Permanent plots of one hectare each were established at each of the three sites. Five individuals of each of the 26 tree species (Table 1) were marked and tagged. On each

**Table 1.** Woody species selected for phenological study. The information on pollination mechanism is from ref 7.

Species	Family	Pollination mechanism
<i>Acacia catechu</i> (L. F.) Willd	Mimosaceae	Psychophily-Sapromyophily-Melittophily
<i>Adina cordifolia</i> (Roxb.) Hook. f. ex. Brandis	Rubiaceae	Psychophily
<i>Aegle marmelos</i> (L.) Correa	Rutaceae	Melittophily (bees)
<i>Anogeissus latifolia</i> (Roxb. ex DC) Wall. ex Bedd.	Euphorbiaceae	-
<i>Bauhinia racemosa</i> Lamk.	Combretaceae	Melittophily (bees)
<i>Boswellia serrat</i> Roxb. ex Colebr.	Anacardiaceae	Melittophily
<i>Briedelia retusa</i> Muell. -Arg	Caesalpiniaceae	-
<i>Buchanania lanzan</i> Spreng	Burseraceae	-
<i>Butea monosperma</i> (Lamk.) Raub	Fabaceae	Ornithophily
<i>Cassia fistula</i> L.	Caesalpiniaceae	Melittophily (Carpenter bees)
<i>Diospyros melanoxylon</i> Buch Ham	Ebenaceae	Cantharophily
<i>Emblica officinalis</i> Gaertn.	Euphorbiaceae	-
<i>Gardenia latifolia</i> Ait.	Rubiaceae	Chiropterophily
<i>Hardwickia binata</i> Roxb.	Caesalpiniaceae	-
<i>Lagerstroemia parviflora</i> Roxb	Lythraceae	Melittophily (bees)
<i>Lannea coromandelica</i> (Houtt.) Merrill	Anacardiaceae	-
<i>Madhuca longifolia</i> (Koen.) Mac Br.	Sapotaceae	Ornithophily-Chiropterophily-Melittophily
<i>Milusa tomentosa</i> (Roxb.) Smclair	Annonaceae	-
<i>Pterocarpus marsupium</i> Roxb.	Fabaceae	Melittophily
<i>Shorea robusta</i> C. F. Gaertn.	Dipterocarpaceae	Melittophily (Carpenter bees)
<i>Soymda febrifuga</i> (Roxb.) A. Juss.	Meliaceae	-
<i>Terminalia alata</i> Heyne ex Roth	Combretaceae	-
<i>Terminalia arjuna</i> (Roxb. ex DC) Wt and Arn	Combretaceae	-
<i>Wrightia tomentosa</i> R. and S.	Apocynaceae	Melittophily-Cantharophily
<i>Xeromphis uliginosa</i> (Retz.) Maheshwari	Rubiaceae	-
<i>Ziziphus qluberrima</i> (Sedgw.) Santap.	Rhamnaceae	Sapromyophily-Melittophily

Pollination mechanism is not known, but are probably pollinated by promiscuous pollinators (S Bhatnagar, pers comm)

individual, four branches were marked with metal tags, and on each branch five twigs were selected and also marked with metal tags. Observations at 30-day intervals were made for each of the tagged individuals for the initiation and completion of the following phenophases: leaf flushing, leaf-fall, flowering, fruiting and fruit-fall.

At the community-level, May constituted the peak period of leafing when 42% species initiated leaf formation at site I, 64% at site II and 56% at site III (Figure 1 b). In July maximum number of species ended leafing; 42% at site I, 57% at site II and 43% at site III. Considerable diversity in leafing occurred among plant species (Table 2). A limited secondary leaf flush occurred in all the species except for *Lannea coromandelica* in September. In *Adina cordifolia*, *Briedelia retusa* and *Hardwickia binata* releasing continued even in October. Significance of releasing is not evident, however. Asynchronous behaviour in leafing was conspicuous among the individuals of *Lagerstroemia parviflora*.

The peak period of leaf-fall initiation occurred in January when 68% species at site I and 43% at site III started shedding the leaves. At site II maximum number of species (50%) initiated leaf-fall in December. Peak period for the end of leaf-fall occurred in March for site I (68%) and site III (71%), and in February for site II (50%) (Figure 1 c). There occurred a considerable diversity in leaf-fall among plant species (Table 2). As a result the community-level leaf-fall continued for six months (February–April). Some species indicated asynchronous behaviour in leaf-fall among their individuals. In *Lannea coromandelica* a majority of individuals started leaf shedding in November, while a few individuals were already naked in this month. In *Gardenia latifolia* a majority of individuals had shed their leaves by March, while a few individuals did not begin leaf shedding till April. *Diospyros melanoxylon* and *Shorea robusta* also showed asynchronous behaviour. None of the individuals in *Shorea robusta* was ever naked on the moist site I, but on the dry site II, for a week or so most of the individuals were naked in March.

At the community-level, May constituted the peak period of flowering at all three sites when 32 per cent species at site I, 42 per cent at site II, and 43 per cent at site III initiated flowering (Figure 1 d). There were two secondary peaks, one in February and the other in July. Diversity in flowering among plant species was marked (Table 2). Although in a majority of species flowering ended between June to August, at community level it was quite staggered; on site I flowers were available from January to August, on site II from January to October and on site III from February to August. Among individuals, asynchronous behaviour in flowering

Table 2. Diversity among plant species in the periods of initiation and completion of phenophases resulting into extended phenophases at the community level.

Species	Leaf initiation	Completion of leaf initiation	Leaf fall initiation	Leaf fall completion	Flowering initiation	Completion of flowering	Fruit initiation	Fruit fall initiation	Completion of fruit fall
<i>Acacia catechu</i>		August							
<i>Aegle marmelos</i>		August			September		October	May	
<i>Anogeissus latifolia</i>									
<i>Bauhinia racemosa</i>		June			January	February	January	April	February
<i>Boswellia serrata</i>	June	August			February	March		December	
<i>Briodelia retusa</i>		August			February	March		April	
<i>Buchanania lanzan</i>			March		February				
<i>Butea monosperma</i>		June			February				
<i>Diospyros melanoxylon</i>		June	February–March	April					
<i>Hardwickia binata</i>		August	March						
<i>Lannea coromandelica</i>		August	November	December–January	January	February	January	March	
<i>Madhuca longifolia</i>									
<i>Milusa tomentosa</i>		August			February	March		August	September
<i>Pterocarpus marsupium</i>		June						October	November
<i>Shorea robusta</i>	February–March	June			August	September		November	January
<i>Soyimida febrifuga</i>					April			May	
<i>Terminalia alata</i>		June							
<i>Wrightia tomentosa</i>		August							
Community peak period	May	July	January	February–March	May	June–August	June	January–February	April–May



was conspicuous in *Acacia catechu* and *Lagerstroemia parviflora*.

At the community-level, peak period for initiation of fruiting occurred in June (Figure 1e). Considerable diversity, however, existed among species (Table 2). Thus the fruiting activity continued for as much as 10 months within the annual cycle. Asynchronous behaviour in fruiting among individuals occurred in *Acacia catechu* and *Lagerstroemia parviflora*.

At the community-level, January–February constituted the peak period for initiation of fruit-fall (Figure 1f). Peak period for completion of fruit-fall occurred in May for site I (42% species) and II (29%), and in April for site III (43%). Considerable diversity existed among plant species in respect of fruit-fall (Table 2). In most of the plant species end of abscission of fruits occurred during March–June but in few species fruit-fall was completed much earlier or much later than this period (Table 2).

The above observations indicate that the dry period is characterized by intense phenological activity in the seasonally dry tropical forest. Initiation of leaf fall coincides with the onset of the post-monsoon, low-temperature dry period and can be a mechanism of maintaining shoot turgidity. However, leaf flushing begins with the rise in temperature and peaks in the hottest and driest month (May) of the year; thus temperature seems to trigger leaf initiation. Studies in certain other tropical areas also indicate that leaf flushing is not correlated with the onset of the rainy season but rather precedes it<sup>8</sup>. In contrast, leaf flushing in dry forests of Ghana is entirely limited to wet seasons<sup>5</sup>. The initial nutrient demand of the emerging leaves is probably met from the pool of nutrients withdrawn earlier from senescing leaves, but there is a conspicuous lack of information on the water demand and supply relationships of the new foliage during the dry period. It can be argued that most of the additional water needed may come from roots located in the deeper soil layer with appropriate reduction in stomatal conductance of the emerging leaves. The dry season leaf flushing nevertheless, permits the renovation of the canopy before the monsoon rainfall begins, such that the plants are able to take full advantage of the short rainy season for primary production and growth. Further, at the community level leaf flushing continued for 7 months (February to August) ensuring continued availability of new photosynthetically-active tissue. This also results in sustained supply of tender food resource to phyllophagous insects which constitute an important component of community food-web and benefit the plants by speeding up the nutrient cycling. Still there was a greater synchrony among species for leaf turnover compared to other phenological activities.

The coincidence of peaks in leafing and flowering is

interesting. Leafless and low-foliage periods are favourable for wind pollination as well as for floral display to attract pollinators. Massive premonsoon flowering also means a continued availability of energy in the subsequent rainy season to developing fruits when the foliage is actively photosynthesizing. In tropical dry forests of Sri Lanka flowering occurred as soil moisture reserves depleted<sup>9</sup>. Two peak periods of flowering activity, one extensive period during the long dry season and a second peak period corresponding to the onset of the rainy season have been reported for Costa Rican dry forest<sup>10</sup>. In dry deciduous woodland in Tanzania tree flowering mainly occurred in the prerains, warm dry period<sup>11</sup>.

Experimental pollinations showed a high proportion of tree species in the dry forest of Costa Rica to be self incompatible; for the obligate outcrossing they depend upon animals for effective transfer of pollen<sup>12</sup>. All the species in the present forest whose pollination mechanism is known are also animal-pollinated (Table 1), and flowering was rather staggered covering a period of 10 months, with two secondary peaks apart from the main May peak. Staggered flowering may be an evolutionary mechanism to avoid interspecific competition for pollinators or to avoid interspecific pollen transfer which could result in reduced pollen donation, reduced seed set (due to stigma clogging) and occurs in less fit hybrids<sup>13</sup>. In the Costa Rican dry forest the flowering periods of a large number of species were spread over 3.5 months to minimize flowering overlap<sup>1</sup>. Community-level flowering for a longer period ensures sustained flow of floral food stuffs to various groups of pollinators whose population may peak at different times in the year. Asynchrony in flowering within species as exhibited by *Acacia catechu* and *Lagerstroemia parviflora* in the present study, promotes outcrossing, reduces intraspecific competition for pollinators and reduces geitonogamy<sup>13</sup>.

The fruiting phenology closely follows the flowering phenology. Consequently this activity was also quite staggered and prolonged at the community level. In the dry forest of southern Puerto Rico, no more than 50% of the 33 species were observed to fruit at the same time<sup>4</sup>. Sequential fruiting permits the dispersal agents to be utilized fully with minimum competition for their service<sup>14</sup>. A close correspondence between flowering phenology and fruit development minimizes the time of exposure to flower and seed predators. At the community level, fruit-fall which begins in January–February is completed in most species before or just at the beginning of the monsoon season. This ensures availability of sufficient moisture to seeds for germination and seedling establishment.

Thus the phenological clock of the dry forest appears to be set during the interphase of winter and summer



enabling the community to take full advantage of the rainy season for productivity and recruitment of plants through germination, while maximising the period of food availability to pollinators, frugivores and seed predators in return for their pollen transfer and seed dispersal services. Factors that may cue phenology in a proximate sense could be water stress, humidity, temperature and timing of nutrient release<sup>15</sup>.

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## HISTORICAL NOTES

# Science in British India. I. Colonial tool

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A major accomplishment of the Renaissance in Europe was the 1498 discovery of the direct sea route to India. The great commercial success of the Portuguese spurred the Dutch, the English, and then the French to venture out to the sea. The overseas trade was extremely profitable<sup>1</sup>. Cloves purchased for only £2048 in the Spice Islands sold in London in 1609 for £36,287. The first 12 voyages to East Indies from England yielded an average profit of 138%. By 1621, one man in 2000 in England was working for the East India Company<sup>2</sup>. The navigational needs of the traders acted as a great incentive for development of science in Europe. The best scientists of the time applied their minds to 'discover the longitude'. In the early seventeenth century, professors at Gresham College, London took up navigational problems in the national interest, e.g. Henry Briggs<sup>4</sup> (1560-1631) whose introduction of logarithm to the base 10 greatly simplified mathematical calculations.

English as well as French companies started compiling sea charts and keeping records of voyages. Observatories were

opened at Paris (1667) and Greenwich (1675) to solve the problem of the longitude. The Astronomer Royal supplemented his meagre salary by giving tuition to young men seeking employment with the East India Company<sup>4</sup>. It paid to join the Company, and it paid to know astronomy.

The European climate was now extremely conducive to scientific innovation. The 1731 invention and use of a sea quadrant by a young American glazier Thomas Godfrey was a dead end because neither the inventor nor America at the time had any use for it. But the next year, when it was independently invented in England (by John Hadley), it was immediately accepted as a valuable navigational aid and developed further<sup>5</sup>. As early as 1736, Hadley's octant 'when it was definitely regarded as an English instrument', was used in India by a French navigator, Apres de Manneville [ref. 6a, p. 151 = 6a:151].

Maritime trade transformed not only European economy but also its state of mind. For the first time in history of mankind, production of wealth depended not upon the courtesy of God and the

King, but on human endeavour. Merchants and artisans now became respectable and influential members of the society. And since the new rich class owed its wealth to science, it became patron of science.

The new experiences weakened the hold of the past authorities. Thus the French physician Julien La Mettrie wrote in 1747 in *The Man-Machine*: 'We are no more committing a crime when we obey our primitive instincts than the Nile is committing a crime with its floods, or the sea with its ravages'<sup>7</sup>.

Modern science came to India in tow with the Europeans. The very act of reaching India from Europe showed a sense of adventure and competence. It was natural for these early visitors to try to acquaint themselves with their new environment, for survival as well as for profit. Early European scientific endeavours in India consisted of two disciplines, geography and botany. In the early days, the Europeans were confined to the coastal areas and had no reason to venture into the interior. Geographical exploration therefore fell to the Jesuit priests. The Society of Jesus was set up