Phenology of trees in a sub-tropical humid forest in north-eastern India*

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Abstract

Phenological observations were made on 122 tree species in a subtropical humid seasonal forest in north-eastern India. The forest had a high proportion of evergreen compared to deciduous species. Leaf-fall of most of the tree species coincided with the dry season. Flushing started towards the end of the dry season for a majority of the tree species, the degree and period of leaflessness varying with the species. Leaf production in the overstorey species extended over a longer period compared to the understorey species. For most of the species, flowering coincided with leaflessness. Proportionately more overstorey species flowered during the dry season and wet season flowering was more characteristic of understorey species. A majority of the species produced fleshy fruits during the wet season. Fruits, produced during the dry season, were mostly dry.

Introduction

Many studies exist on general phenological patterns (Janzen, 1967; Nevling, 1971; Medway, 1972; Daubenmire, 1972; Croat, 1975; Putz, 1979) and breeding systems (Smythe, 1970; Bawa, 1974; Ashton, 1977; Ruiz & Arroyo, 1978) of tropical forests at a community level. The displacement and adjustment of flowering and fruiting of different species in time and space for the efficient utilization of pollinators (Levin & Anderson, 1970) and seeddispersal agents (Janzen, 1970; Arroyo, 1979) are important for niche differentiation in a forest community. Recently, attention has also been paid to the relationship between phenological patterns and the strategies of vegetative growth and reproduction (Frankie *et al.*, 1974; Hilty, 1980; Arroyo *et al.*, 1981). However, most of these studies are mainly confined to tropical regions with slight seasonal changes. The sub-tropical forests with distinct seasons are little explored. An understanding of the phenological events in a forest community may reveal the structural organization of various types of resources in the ecosystem.

The present study was undertaken as little information on phenology is available on sub-tropical humid forests of NE India (Singh, 1980) characterized by a high species richness. The study site at Lailad (25°45″–26°N lat. and 91°45″–92°E long.) has been maintained as forest reserve by the local Forest Department for about 50 yr. It is located about 70 km N of Shillong at 296 m altitude in the Khasi Hills of Meghalaya.

Climate and vegetation

The climate of the area is typically monsoonic with most (84%) of the total average annual rainfall

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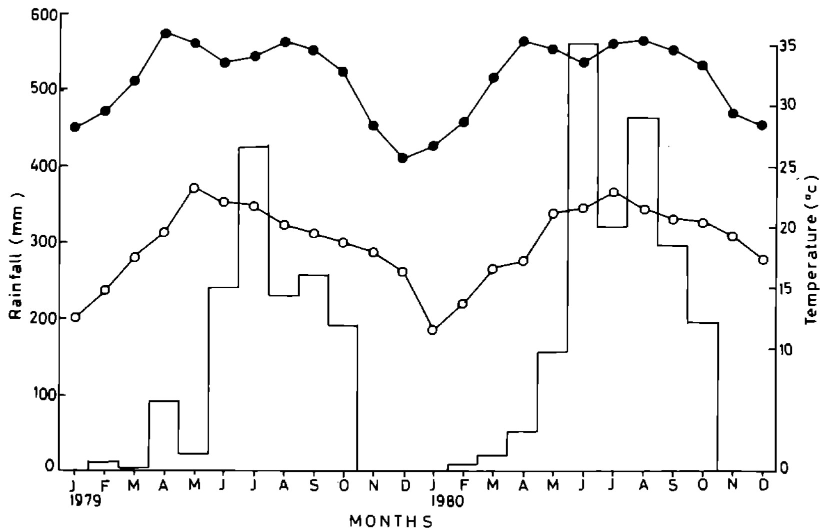

Fig. 1. Ombro-thermic diagram for the study site. —, rainfall; ●—●, mean daily maximum temperature and O—O, mean daily minimum temperature.

of 2 200 mm between May and September. There is also some rainfall during April and October, while the remaining months are dry. The monsoon season, with high humidity, is followed by a mild winter during November to mid-February. From mid-February to early April there is a dry summer period with strong wind currents (Fig. 1).

The forest overstorey is composed chiefly of *Schima wallichii, Castonopsis indica, Shorea robusta, Tetrameles nudiflora, Elaeocarpus* spp., *Miliusa roxburghiana, Artocarpus chaplasha, Vitex peduncularis, Mesua ferrea, Amoora wallichii* and *Garcinia* spp. The more frequent understorey trees are *Croton oblongifolius, Oroxylum indicum, Goniothalamus simonsii, Unona longifolia* and *Heptapleurum hypoleucum. Croton caudatus, Litsea lancifolia* and *Randia wallichii* are the dominant shrubs. It may be noted that there were no potentially overstorey species as understorey trees. The important herbaceous species are *Panicum khasianum, Cyperus elegans, Fimbristylis dichotoma, Hedychium gracile* and *Passiflora nepalensis* with the forest opening being dominated by *Eupatorium odoratum, Lantana camera* and *Mikenia micrantha.*

Methods of study

General phenological observations were made on 122 tree species representing >60% of the tree species of the area. A few selected trees of each species were tagged with aluminium labels for detailed observation at 2-weekly to monthly intervals. Records on leaf fall, flushing, flowering activity and fruiting activity were made. A species was considered to be passing through the peak of a phenophase when more than 50% of the individuals of that species did so.

The trees were divided into two categories: (a) Overstorey species in canopy and subcanopy (b) understorey species <15 m tall (Frankie *et al.*, 1974). The pattern of leafiness of the trees was classified into three groups: (i) evergreen-evergrowing type, which continually produces small quantities of new leaves showing no heavy leaf-fall at a given time, (ii) evergreen-periodic type which has a leaf-fall and flushing period each year and (iii) deciduous type which become completely leafless for at least a brief period of time and show peak leaf-fall and flushing at certain times of the year. The general phenological features are summarized in the text but detailed information on individual species characteristics is available on request from the authors.

Results

Leafing activity

The humid forest at Lailad maintains its green appearance throughout the year with many evergreen tree species including a few evergrowing types. In the dry months from January to March, many species drop their leaves. Flushing and leaf production occur during subsequent months upto September. About 40% of the total leaf litter of 4.3 t/ha is reported (Singh, 1980) to accumulate in the drier period of February to March. In other months leaf-drop is comparatively low.

Leaf-fall

The peak of nakedness was achieved during March in both overstorey and understorey species. None of the tree species in either the understorey or overstorey showed conspicuous leaf-drop during the peak monsoon period of June–July (Fig. 2a). A few species like *Cedrela toona, Baccouria sapida* and *Elaeocarpus* spp. amongst the overstorey and *Croton* spp. and *Styrax serrulatum* amongst understorey, dropped their leaves primarily during August and September. An understorey species, *Aesculus assamica* became naked during November–December.

Flushing

Periodicity of flushing in different species (Fig. 2b) indicates that the peak period coincides with the end of the dry season and the start of monsoon. For the overstorey species peak flushing occurred in April whereas this was delayed a month for the understorey species. In general, the time for bud burst or first flushing extended from February to June except in the case of the understorey species, *A. assamica* which flushed during December and a few evergrowing species like *Calicarpa arborea, Saprosma ternatum* and *Duabanga sonneratioides* which produced some leaves throughout the year.

The observation on cessation of growth in a few selected over- and understorey species showed that leaf production in many of the overstorey species was over by September–October but the understorey species stopped leaf production by August–September. Thus there was a time lag of nearly a month between the growth cessation of over- and understorey species (Table 1).

Flowering activity

All the species observed bloom once a year and the flowering period of most of the species (seasonally-flowering) extends to about 8 weeks starting from bud inception to full bloom stage. For conven-

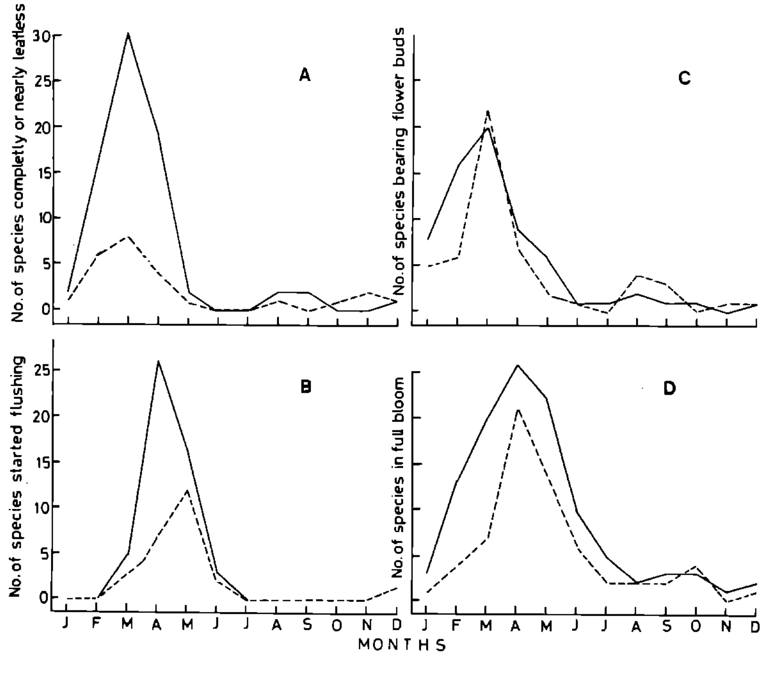

Fig. 2. Phenological periodicity of overstorey (—) and understorey (---) tree species; 2a) leaf fall; 2b) flushing; 2c) flower bud; 2d) flowering.

Table 1. Cessation of growth (leaf production) in some over- and understorey tree species.

Tree species	Growth cessation
Overstorey:	
Amoora wallichii King.	Oct. I–II
Anthocephalus cadamba Miq.	Oct. II–Nov. II
Artocarpus chaplasha Roxb.	Oct. II–Nov. I
Castanopsis indica A.DC.	Sept. III–Oct. I
Chukrassia tubularis A. Juss.	Oct. II–Oct. IV
Gmelina arborea L.	Sept. III–Oct. II
Lagerstroemia parviflora Roxb.	Sept. I–III
Mesua ferrea L.	Aug. II–Sept. I
Shorea robusta Gaert.	Aug. III–Sept. II
Sterculia villosa Roxb.	Oct. I–II
Vitex altissima L.	Sept. III–Oct. I
Understorey:	
Actinodaphnae angustifolia Nees.	Aug. III–Sept. I
Bauhinia malbarica Roxb.	Sept. I–II
Lagerstroemia flos-reginae Retz.	Aug. IV–Sept. II
Oroxylum indicum Vent.	Sept. I–II
Pithecolobium longan Benth.	Aug. I–II
Premna miliflora Clarke.	Aug. II–Sept. I
Styrax serrulatum Roxb.	Aug. II–III

I, II, III & IV refer to different weeks of a month.

ience, therefore, the flowering activity is divided into bud stage and blooming stage. A few species flower for periods of several months covering more than one season (extended-flowering).

Flower bud inception

The period of peak for flower bud inception coincides with that of peak leaf-fall in February–March in both the over- and understorey species, irrespective of whether they are deciduous or not. The flower bud initiation of the overstorey species starts vigorously in January–February though it peaks in March for both under- and overstorey species with a sharp decline in April–May. In subsequent months bud initiation is maintained at a very low level though the understorey species has a smaller peak in August–September (Fig. 2c).

Table 3. Number of over- and understorey species in flowering stage during dry and wet season.

	Dry season	Wet season	Extended flowerers	data incomplete
Overstorey	24	48	2	2
Understorey	9	29	2	6
Total	33	77	4	8

Flowering

As a consequence of the pattern of flower bud development, the peak flowering among both the over- and understorey species is attained in April after which it declines sharply and is maintained at a low level beyond July (Fig. 2d). A large number of overstorey species flowered during the dry season ($\frac{24}{74}$) whereas only a smaller fraction of understorey species flower at this time ($\frac{9}{40}$). However, a large number of understorey species flower during the rainy season ($\frac{29}{40}$) compared to overstorey species ($\frac{48}{74}$). Considering all the species together it can be seen that flowering is more during the wet season ($\frac{77}{114}$ VS $\frac{33}{114}$) as shown in Table 3.

Flowering behaviour

Most of the species like *Morus laevigata, Eugenia* spp. and *Pithecolobium longan* have a short flowering period of only about 2–7 weeks while a few species like *Duabanga sonneratioides, Schima wallichii, Calicarpa arborea* and *Aesculus assamica* show an extended flowering period of about 20–27 weeks. However, the peak flowering in *D. sonnera-*

Table 2. Types of leafing activity of tree species.

Group	Activity	Number of species	
		Overstorey	Understorey
Evergreen-evergrowing	Continuous leafing	3	1
Evergreen-periodic	Discontinuous production of leaves	28	36
Deciduous	Marked leaf fall and flushing	45	9
Total		76	46

tioides and *Schima wallichii* is pronounced during January–February and May–June respectively but the peak of flowering in *C. arborea* and *A. assamica* extend for about 8 weeks. While no significant difference in flowering pattern was observed for a given species from one year to another, individuals within the species showed differences in the vigour of flowering from year to year as seen from observation over a 2 year period. Vigour may be more or less for an individual of a given species such as *Cedrela toona, Casearia glomerata, Anthocephalus cadamba,* or the individuals that flower in one year may not flower at all in the next year as in *Mesua ferrea, Myristica linifolia, Mangifera indica* and *Artocarpus chaplasha.*

Fruiting activity

The fruiting period may be divided into two parts: (i) fruit development and (ii) fruit ripening and fall. The fruiting period extends over a few months both for seasonal as well as extended flowering species.

Fruit development

A number of species of both stories shed their flowers in March when fruit development starts so that the peak of fruit development is in June. However, the developmental period for fruits of different species extends from 5 to 20 weeks. The pattern of fruit development is nearly the same in both the over- and understorey species. The number of species from both the stories with growing fruits (Fig. 2e) reaches a maximum during the rainy season.

Fruit ripening and fall

The peak for fruit ripening and fall occurs in the months of July and August, though quite a few species shed their fruits in May–June or in September–October. Fruit ripening and shedding beyond this period is very low (Fig. 2f).

Fruiting behaviour

All the species that show extended flowering as well as a few others like *Oroxylum indicum* and *Hydnocarpus kurtzii* bear fruits for more than 20 weeks while the rest of the species have brief fruiting periods of not more than 6–10 weeks. The proportion of tree species fruiting in dry months ($\frac{16}{118}$) is very low in comparison to those fruiting during wet months ($\frac{96}{118}$). During dry periods, fruiting in overstorey species is somewhat less ($\frac{9}{76}$) in comparison to understorey species ($\frac{7}{43}$) as shown in Table 4.

Table 4. Number of overstorey and understorey tree species bearing mature fruits during dry and wet season.

	Dry season	Wet season	Extended fruiters	data incomplete
Overstorey	9	63	3	1
Understorey	7	33	3	3
Total	16	96	6	4

In the community, species producing fleshy fruits are markedly higher in number than those producing dry fruits ($\frac{72}{118}$ VS $\frac{46}{118}$). During wet months, a majority of the species produce fleshy fruits ($\frac{65}{96}$) as compared to those yielding dry fruits ($\frac{31}{96}$). During dry months, the number of species producing fleshy fruits was less than producing dry fruits ($\frac{4}{16}$ VS $\frac{12}{16}$; Table 5).

Discussion

The phenological observations on the species and climatic characteristics of the study site suggest that this community is a semi-deciduous seasonal forest with majority of understorey and several overstorey species being evergreen. Correlation of phenological characteristics with naturally occurring climatic events may be best documented by the pattern of leaf-fall. The period of greatest leaf-fall coincides with the relatively xeric conditions of the dry season during the summer (March–April). There are several reports of maximum leaf-fall during the driest

Table 5. Number of overstorey and understorey tree species producing dry and fleshy fruits during dry and wet season.

	Dry season		Wet season		Extended fruiters		Data incomplete
	D	F	D	F	D	F	
Overstorey	6	3	21	42	2	1	1
Understorey	6	1	10	23	1	2	3
Total	12	4	31	65	3	3	4

D = Dry fruits.
F = Fleshy fruits.

part of the year in different tropical forest types (Richards, 1952; Frankie *et al.*, 1974). While peak leaf-fall occurs during the brief summer, many of the emergent species start shedding their leaves earlier during the dry winter season itself. Thus overstorey species like *Sterculia villosa* and *Tetrameles nudiflora* became naked by January–February while the understorey species like *Garcinia cowa, Miliusa roxburghiana* and *Ilex excelsa* have the peak leaf fall only by March–April. This may be related to micro-environmental differences such as insolation (Richards, 1952).

Flushing and leaf production start towards the end of the dry season, frequently before the beginning of the rains. This has also been shown for other seasonal tropical forests (Boaler, 1966; Frankie *et al.,* 1974). Walter (1968) attributes the pre-rain flushing to the triggering effect of the rising temperature. This may also be applicable to the present study but such a correlation was not observed in the tropical forests of Costa Rica (Daubenmire, 1972) and Malaysia (Putz, 1979). Others have implicated day length increase as the inducer of flushing (Njoku, 1964; Lawton & Akpan, 1968) which is true for the present study during March–April.

Though bud-burst is a pre-monsoon event, leaf production is maximal during the early part of the rainy season in May. The present results suggest three distinct strategies of leaf replacement. A large proportion of overstorey species exhibit dry season leaf-fall-dry season flushing while the understorey species, generally, have dry season leaf fall – wet season flushing. The continuous leaf fall – continuous flushing strategy of leaf replacement was observed only in a few species like *Duabanga sonneratioides, Saprosma ternatum* and *Anthocephalus cadamba.* The former two strategies that predominate here have been suggested to be adaptive to small seasonality in temperature and large seasonality in moisture regime (Jackson, 1978) as occurs in the present study area. The cessation of growth in different species occurr with the fall in temperature and decrease in day length. It may be noted that photoperiod (Njoku, 1963; Hopkins, 1970) and its interaction with temperature (Thimann, 1962) have been implicated to control apical bud dormancy.

Synchronization of flowering with dry season seems to be under the control of prevailing climatic conditions. A similar periodicity has also been observed in rain forests (Richards, 1952; Medway, 1972). However, such a seasonality in flowering could not be recognised in the forests of Malaysia (Putz, 1979) and Columbia (Hilty, 1980). Apart from moisture-related factors (Opler *et al.*, 1976), a change in photoperiod has also been suggested to trigger flowering (Njoku, 1963; Lawton & Akpan, 1968).

Peak fruiting in this forest occurs during the wet season, most of the species producing fleshy fruits with large seeds. The need of high moisture level for the proper development of fleshy fruits has been reported by Zahner (1968) who showed experimentally that the shortage of soil-moisture reduced the rate of enlargement and final size of these fruits. High moisture level during the wet season also favours germination and establishment. Most of the dry season fruiters including some extended fruiters like *Duabanga sonneratioides* and *Schima wallichii,* generally produce small winged seeds whose dissemination is favoured by wind current during the dry summer. It may be noted that Smythe (1970) indicated a fundamental difference in selection pressures on large- and small-seeded species of a neotropical forest.

Differences in flowering and fruiting patterns among different genera and species suggest the importance of animal-plant interactions. Maximum flowering activity during the warm period with the beginning of the rains may be related to the high insect population as pollen vectors as suggested by Janzen (1967) and Stiles (1978) working in tropical forests. Further, blooming of congeneric species like those of *Eugenia, Garcinia* and *Litsea* do not coincide substantially, in a manner to avoid competition for common pollen vectors. Since in the tropics, animal pollination is more frequent than wind pollination (Whitehead, 1969) and the tropical trees are mostly self incompatible (Bawa, 1974), the coincidence of flowering with the relative leaflessness of the canopy may facilitate insect pollination by enhancing visibility and easy access to the flower (Janzen, 1967). Further, alternate yearly or irregular flowering as observed here for some species may also be significant as an escape 'from seed predation on a time basis' (Janzen, 1970). Thus, the unified analysis of the leafing, flowering and fruiting periodicities in this forest suggest that the species organization of the community with an assemblage of different patterns of phenophases fit well for a balanced ecosystem function.

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