COMPARATIVE PHENOLOGICAL STUDIES OF TREES IN TROPICAL WET AND DRY FORESTS IN THE LOWLANDS OF COSTA RICA

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INTRODUCTION

The dearth of plant phenological studies in tropical latitudes has been pointed out by various authors (Gibbs & Leston 1970; McClure 1966; Nevling 1971; Rees 1964). A review and brief evaluation of the few available investigations is presented by Frankie, Baker & Opler (1974). In most of these studies, a partial analysis of leafing, flowering or fruiting data is offered for a limited number of species and for limited time periods only.

The results of a comparative phenological investigation of the trees in Wet and Dry forest sites in lowland Costa Rica are reported here. An attempt has been made to provide a unified analysis of the leafing, flowering, and fruiting periodicities of most species at both sites. The Wet forest site, Finca La Selva, is situated in the Atlantic watershed, while the Dry forest site, Comelco Property, is situated in the Pacific watershed.

The study, which began in 1968, is part of a larger investigation aimed at analysing the biological organization of Wet and Dry forest ecosystems from the standpoint of plant reproductive biology.

In this study the definition of a tree put forward by Lindley & Moore (1884, p. 1161) as 'any woody plant of perennial duration which rises from the ground with a trunk' has been adopted in part. To this we have added a minimum height qualification of approximately 3 m.

We were unable to recognize distinct layers within the forest canopy at either site. Stratification, in which three or more tiers are generally designated, has been described by investigators working in various Tropical Rain forests (Beard 1955; Jones 1955; Lundell 1937; Richards 1952; Webb 1959). Other workers have been unable to discern definite layers clearly (Cain & Castro 1959; Grubb *et al.* 1963; Paijmans 1970; Schulz 1960). However, because trees are subject to different environmental conditions depending upon their position in the canopy and also for ease in recording data, tree species at the Wet forest site were arbitrarily divided into two categories: overstorey and understorey species. The first group consisted of canopy and subcanopy species, with the understorey comprising trees generally less than 15 m in height. Croat (1969) also divided trees at Barro Colorado Island into two layers for similar reasons.

No layering effect was observed in the Dry forest and, because of the lesser tree heights, all trees in this forest were considered to belong to a single layer.

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STUDY SITES

Wet forest site: La Selva

The La Selva property is a roughly rectangular, 700 ha area of largely undisturbed Lowland Rain forest and is located at about 140 m altitude in Heredia Province (latitude $10^{\circ} 25'$ N, Fig. 1). The northern half of the property is largely flat while the southern half, though partly flat, has numerous rolling hillocks. La Selva has several swampy areas and two major streams. Included within its boundaries are some small second growth areas at the northern border and one relatively large second growth stand to the east. The northern boundary is entirely defined by the Río Puerto Viejo which joins the Río Sarapiqui at the far north-western corner of the property. To the west and to the south the property is bounded by undisturbed forest. Other general descriptions of the site are given by Bourgeois *et al.* (1972), Holdridge *et al.* (1971), McColl (1970), Petriceks (1956), Sawyer & Lindsey (1971) and Slud (1960).



FIG. 1. The locations of study sites in the Atlantic (Wet) and Pacific (Dry) lowland forests of Costa Rica.

La Selva climate

Appreciable rainfall occurs at the Wet forest site in every month. The mean annual precipitation for the period 1958–71 was c. 4000 mm, with a range from 2900 to 5600 mm. Generally there is one long dry season from late January until April and a second, less noticeable, dry season from August until October (Fig. 2). The first wet season begins in late April and extends into the first part of August. The second wet season lasts from November through most of January.

Deviations from the usual dry and wet seasons were recorded during the study period. In 1969 the first dry season was quite severe and of long duration while the second dry season was normal, but of short duration (Fig. 2). In 1970, rainfall was unusually heavy during the first and last parts of the long dry season and during the middle of the second dry season.

Monthly mean temperature is 24° C (Fig. 2); there is a difference of about 6-12° C between the mean maximum and mean minimum daily temperatures of any month.

La Selva vegetation

La Selva forest vegetation can be broadly characterized as Tropical Rain forest, as conceived by Leopold (1959), Odum (1970) and Richards (1952). According to the Holdridge Life Zone System, the La Selva formation is geographically and bioclimatically situated so as to overlap the boundary between Tropical Wet Forest and Premontane Wet Forest life zones (Holdridge 1967; Holdridge *et al.* 1971; Tosi 1969).



FIG. 2. Annual distribution of the mean monthly, mean monthly maximum and mean monthly minimum temperatures (October 1969 to August 1971) and of rainfall (1958–1971) at the Wet forest site (La Selva), Heredia Province (detailed rainfall figures are given for 1969 and 1970). Temperature records compiled by G. S. Hartshorn (1972); those for rainfall by P. Slud (unpublished).

Six broad community-types are recognizable: undisturbed Wet forest, Swamp forest, Riparian forest, light gaps in Rain forest, open water swamp, and second growth. Descriptions of only the first three types are given since subsequent papers will report on the other communities.

(i) Undisturbed Wet forest. Most of La Selva is covered by high, apparently virgin forest with some emergent trees reaching over 50 m in height. Below the discontinuous canopy, other trees form a continuum, without definable stratification. Most species are evergreen and have straight trunks and, according to Holdridge *et al.* (1971), 64% of all the tree species have well-formed plank buttresses. This community contains the greatest diversity of tree species. Holdridge *et al.* (1971) recorded sixty-five species in a sample area of 8000 m². The families Leguminosae, Rubiaceae, Palmae, Moraceae, Euphorbiaceae, Annonaceae, Tiliaceae and Myristicaceae are well represented with several species each. The most common species is *Pentaclethra macroloba*,* which forms about 40% of the basal area (Hartshorn 1972). A total of ninety-three species was recorded in the overstorey and ninety-two in the understorey (see Appendix, Lists 1 and 2 re-

* Authorities for all scientific names are given in the Appendix, Lists 1-3.

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spectively). Lianas are uncommon except in certain locations where they can become abundant on large trees. Epiphytes are common at all heights. At lower levels in the forest, shrubs and tall herbs are more or less continuous (Slud 1960).

(*ii*) Swamp forest. This has a closed canopy. Typically there is standing water all the year round but during rainless periods some sections tend to dry out. Tree species diversity is lower in this community. The three most common tree species are Carapa guianensis, Lecythis costaricensis and Pentaclethra macroloba. In the understorey, palms are quite common.

(iii) Riparian forest. This lines the streams and the river. Pithecolobium longifolium, Ficus spp. and Ochroma pyramidale are common tree species. Other species of the undisturbed forest are occasionally observed along the margins of the water courses, especially along the streams.

Dry forest site: Comelco Property

The Dry forest study site comprises some 20 250 ha of a combination of forest, derived savanna, seasonal swamp, riparian forest, pastureland, and second growth vegetation. The centre of this area is situated approximately 15 km south-west of the town Bagaces, in the province of Guanacaste (Fig. 1).

A series of steep hills, running north-west to south-east, divide the property into northern and southern sections. The northern portion is a flat plateau that extends approximately 10 km south of the Pan American Highway with the northernmost edge at 10° 32' N latitude. Mean elevation above sea level in this area is 90 m. The southern section is largely a lowland area interspersed with small hills (mostly at the far south end). Mean elevation of the lowland area is about 5 m. The main branches of the four river systems on or bordering the property have running water all the year round; however, all small streams dry up during the long dry season that extends from November to May. Holdridge *et al.* (1971) and Sawyer & Lindsey (1971) have described the area and its vegetation.

Comelco climate

All rainfall, temperature and humidity data presented here were provided by a weather station located 4.5 km north of Cañas at Hacienda La Pacifica, which is situated c. 24 km east of the central point of the Comelco Property. These data were used since La Pacifica is within the confines of the Guanacaste Dry forest and generally seem to reflect the climatological pattern at Comelco. Wolf (1970) also used La Pacifica weather data for his ornithological studies at La Granja Experimental Jiménez (14 km south-west of Cañas).

Four seasons are recognizable in the Guanacaste Dry forest, based on relatively wet and dry periods (Fig. 3). Most precipitation falls in the first wet season (late May–early July) and the second wet season (late August–early November). During the rainy seasons, rain usually falls during the afternoons only. For the period 1960–70, the mean annual rainfall was 1533 mm, the highest and lowest values being 2266 and 1007 mm.

The first dry season, which is long and severe, begins in November and extends into May. A second shorter dry season generally occurs in July and August. In some years (e.g. 1965) it may persist for longer but in other years (e.g. 1970) the short dry season never develops (Fig. 3). The first two months of the long dry season are marked by overcast skies and occasional light showers.

The mean monthly temperature is 28° C and variation of the mean from month to



FIG. 3. Annual distribution of the mean monthly, mean monthly maximum and mean monthly minimum temperature and rainfall (1960–1970) at the Dry forest site (Hacienda La Pacifica), Guanacaste Province (detailed rainfall figures are given for 1969 and 1970).

month is approximately 1° C (Fig. 3). The difference between mean monthly maxima and mean monthly minima is no more than 10.5° C. The hottest (and driest) weather occurs in March-April, while the coolest occurs during the latter part of the second wet period and first part of the long dry period.

Data for relative humidity are given in Table 1. The driest months are from February to mid May. However, noticeable drying of the air is felt as early as late November. Between late May and June the relative humidity increases markedly owing to the start of the first rainy period. Surprisingly, the air remains quite moist during the short dry season.

Comelco subsites and vegetation

The Comelco site can be broadly classified as Tropical Deciduous forest. According to the Holdridge Life Zone system the northern plateau is mostly Tropical Dry Forest, Moist Province Transition and Premontane Moist Forest, Basal Belt Transition, while the southern section is predominantly Tropical Dry Forest (Holdridge *et al.* 1971). The northern section consists of irregular areas of disturbed forest, derived savanna, riparian forest, pastureland, and second growth vegetation. The southern section is mostly seasonal swamp vegetation. Forest trees are found on some of the small hills near the southern border. Limited secondary growth and pastureland are also present, but derived savanna and riparian vegetation (except along some parts of the Río Tempisque) are lacking.

Because of the mixture of vegetation types at the Dry forest site, subsites were utilized in eight areas within the property. All subsites contain forested land and all have been

Table 1. Monthly relative humidity recorded at the Dry forest (Hacienda La Pacifica), Guanacaste Province, 1962–67 (daily records based on average of 07.00 h and 18.00 h readings)

	J	F	Μ	Α	Μ	J	J	Α	S	0	Ν	D	Year
Mean	72	66	67	68	71	82	79	81	85	81	78	75	75
Mean maximum	87	83	84	84	89	97	96	97	97	98	94	85	91
Mean minimum	54	47	47	47	48	59	59	57	59	58	57	62	55

disturbed somewhat by cutting, over-grazing, and/or fire. Transects were established in three subsites. The five remaining subsites were used for making monthly assessments of phenological changes in populations of certain species.

Trees of Comelco forests form a discontinuous canopy in which no distinct stratification can be recognized. Emergent Dry forest trees attain heights of 20–25 m, and some riparian species occasionally reach 35 m. Most trees, with the exception of riparian species, lose their leaves during the dry season. Palms do not form an important part of the forest vegetation. Buttressed trees are uncommon (Holdridge *et al.* 1971). The shrubs in the less disturbed forested subsites are widely spaced beneath the trees. Below the shrub layer the vegetation is greatly disturbed owing to periodic burning and grazing that occur at all subsites. Lianas are occasional to rare; often their presence in tree canopies is noticed only when they flower. Epiphytes are relatively scarce in the Dry forest except on trees on soils retaining moisture longer than average.

Six community-types have been recognized in the present study: Moist Deciduous forest, Dry Deciduous forest, Riparian forest, derived savanna, second growth and Seasonal Swamp forest. All communities except the Seasonal Swamp were included in the Dry forest study. The species involved (113) are given in the Appendix, List 3. (i) Moist Deciduous forest. This is situated in areas which receive more water or retain it for relatively long periods of time, such as valley bottoms, high alluvial areas and deep soil sites. The largest trees of this community reach 25 m in height; only a few species are buttressed. Common trees in this community include: Apeiba tibourbou, Chomelia spinosa, Casearia aculeata, Eugenia salamensis var. hiraeifolia, Cordia alliodora, and Tabebuia neochrysantha.

(*ii*) Dry Deciduous forest. This is floristically similar to type (i) but it differs from the latter in having generally a lower height, lesser density and fewer species. Soils of the Dry Deciduous communities receive or retain less water than the Wet Deciduous sites and are usually marked by shallow soils, on dry ridges or rocky outcrops. In addition to most of the common species listed for type (*i*), one or more of the following species will usually be encountered in a Dry Deciduous community: Plumeria rubra, Lonchocarpus eriocarinalis, Rehdera trinervis and Laetia thamnia.

(*iii*) *Riparian forest*. The riparian community is the most complex of the Dry forest communities and is the one most similar in structure and complexity to the undisturbed Wet forest at the La Selva site. Tall trees together with a closed canopy typify riparian vegetation, occasionally reaching 35 m; the trees are in leaf for most of the year. In the understorey an open layer of shrubs is recognizable. Lianas, vines and epiphytes are more common in this community than in other Dry forest communities.

(iv) Derived savanna. The northern section contains several irregular areas in which the vegetation approaches, in physiognomy, a savanna formation. The community is mancreated. Fires, which occur annually throughout Comelco and in most other areas of the Dry forest, maintain or extend this savanna. The vegetation consists of grasses, occasional shrubs and frequent trees. Often the trees and shrubs occur in clumps in which several species are represented. Examples of the common tree species are Byrsonima crassifolia, Curatella americana, Dalbergia retusa, Enterolobium cyclocarpum, Pithecolobium saman, Simarouba glauca, Sweetia panamensis and Tabebuia rosea. Hatheway & Baker (1970) reported on the autecology of Enterolobium cyclocarpum and Pithecolobium saman in such derived savanna communities.

(v) Second growth. More or less isolated sections of second growth vegetation are found throughout Comelco Property. The stands range in age from one to 15 years with most of

nds have occasional to frequent tre

the younger stands devoid of trees. The older stands have occasional to frequent trees, many of which are mature. Common tree species of this community are: Cecropia peltata, Cochlospermum vitifolium, Godmania aesculifolia, Lonchocarpus nitidus and Muntingia calabura.

PROCEDURE

Collection of data

Trees were marked and were observed with binoculars at monthly intervals. In addition to the tagged trees, a monthly assessment was made of phenological changes on a population basis for many species at both sites. At the Wet forest site, the observation period extended from November 1968 to December 1970 and at the Dry forest site from April 1969 to July 1970. Supplementary notes on most species populations were collected at both sites from 1971 to 1973.

For each tagged tree, records were made of leaf development, leaf fall, flowering and fruiting. Only two categories, to signify the amount of activity ('few' and 'many'), were used because of the difficulty of determining quantitatively several different levels. This two-level categorization also alleviated problems of dealing with various sized individuals and the varying intensities of phenological response found occasionally for certain species in different subsites. The proportion of buds to open flowers and the proportion of immature to mature fruits were also recorded.

At the Wet forest site 468 trees, comprising 185 species (see Appendix, Lists 1 and 2), were tagged with aluminium labels; this sample represents >75% of the overstorey species and c. 65% of the understorey species (data of G. S. Hartshorn, personal communication). Species not included in the observations were only very rarely encountered. The average replication of 2.5 individuals per species might not be considered adequate for a study of tropical plant phenology. Because of intrinsic variation as well as habitat differences among members of a population, a minimum of five trees per species should be observed. However, monthly assessments of many populations together with additional observations made on unmarked trees helped to alleviate replication deficiency in the present study.

At the Dry forest site seventeen 200 m transects were randomly established in three different study subsites. An approximately equal number of transects was set up in each subsite by marking with aerosol paint all the mature trees that stood within 5 m to one side of each transect. A total of 1137 trees, comprising 113 species, were numbered for continuous observation (Appendix, List 3). Replication of 10.2 trees per species was considered more than adequate for this study. About 80% of the species in the communities studied at the Dry forest site were represented; the remaining 20% were all rare.

Voucher specimens of all tree species have been deposited at the Chicago Field Museum (Illinois), Missouri Botanical Garden and the Universidad de Costa Rica. Vouchers of most species have also been deposited at the Museo Nacional de Costa Rica and the University of California, Berkeley.

Phenological observations

Methods and problems associated with describing flowering activity have been discussed by earlier investigators working with phenological data in tropical and temperate zones (Anderson & Hubricht 1940; Caprio 1966, 1967; Croat 1969; Hopp, Vittum & Canfield 1969; Royal Meteorological Society 1892–1948). The difficulty in describing flowering periodicity stems from the various manners in which data are collected as well as from the way in which those data are used.

In this study, 'peak flowering period' is used to describe flowering activity for two reasons. Firstly, most tree species in both forest ecosystems displayed distinct periodicities in flowering which were relatively easy to record. Secondly, in later studies floral periodicities will be compared with pollinator periodicities for possible correlations. Comparisons of rather distinct peaks in activity will then be more appropriate than 'times of first flowering' or 'overall periods of flowering' (cf. Croat 1969). For most species the peak in flowering was taken to be when 50% or more of the individuals in a population were producing large quantities of flowers. However, recognition was also given to those species that produced flower crops more than once during the year and to those that flowered over extended periods regardless of whether they produced large quantities of flowers or not.



FIG. 4. Leaf fall periodicity of Wet forest tree species. Overstorey trees, continuous line; understorey trees, pecked line.

Germination studies

Seeds were collected from all species producing fruits for making reference seed collections and various kinds of morphological and chemical analyses, as well as for germination studies. Germination experiments were conducted at the Wet forest site in screen-covered plastic basins filled with 50% sand and 50% soil, a combination which provided for adequate moisture retention as well as drainage. The basins were placed in the shade at the forest edge on louvered tables to facilitate drainage and to allow for protection against animals. Seeds were spread evenly over the soil mix and allowed to germinate for periods up to twelve months.

RESULTS: WET FOREST SITE

Leafing activity

The Wet forest of La Selva maintained its evergreen appearance throughout the year with many of the tree species continually producing a few new leaves. However, in the dry months from February to April changes in several species, in the form of leaf drop and flushing, became noticeable. During severe dry seasons (e.g. 1969), significant accumulations of leaf litter were observed on the forest floor; in 'wetter' dry seasons (see 1970, Fig. 2), the number of leaves falling appeared to be less.

Leaf fall periodicity

Amongst the deciduous species there was a definite tendency for leaf drop to occur during the first dry season in both overstorey and understorey trees (Fig. 4). The greatest



FIG. 5. Leaf flushing periodicity of Wet forest tree species. Overstorey trees, continuous line; understorey trees, pecked line.

amount of leaf fall in the overstorey occurred from January to May, and in the understorey from February to March. Each species differed in time of leaf fall and the period during which the individual trees remained leafless.

Loss of leaves in the understorey was almost negligible when compared with that from overstorey trees. Leaf drop in overstorey trees was first noticed in November, the month having the second highest rainfall. Loss of leaves increased noticeably from November to January despite the occurrence of high precipitation at that time.

After the February peak in leaf fall, the number of species losing leaves declined gradually as the amount of rainfall increased monthly from late March to July. During the second dry season, from August to October, the amount and frequency of rain decreased noticeably with no corresponding leaf drop in any of the species.

Leaf flushing periodicity

Periodicity of those species which produced numerous new leaves at intervals is plotted in Fig. 5. Peaks of leaf flushing coincided with the middle portions of the two dry seasons (February and September), with less in the latter season. All species except *Erythrina cochleata*, which flushed new leaves only during the second dry season, produced many new leaves during the first dry season.

Types of leafing behaviour

Tree species were classified into three groups (Table 2): Group I, species which continually produced small quantities of new leaves and showed no concentrated leaf drop; Group II, those which alternated between the production of many, few or no new

Table	2.	Types	of	leafing	activity	of	Wet	forest	tree	species	(see	text	for
		i	moi	re detail	led defin	itio	ns of	the thr	ee gr	oups)			

		Number of species			
Group	Activity	Overstorey	Understorey		
I	Continuous leafing	26	37		
II	Discontinuous production of new leaves	37	44		
III	Marked leaf drop and flushing	25	7		
	Data incomplete	5	4		
	Totals	93	92		

leaves and showed no concentrated leaf drop or leaflessness; Group III, those with marked leaf drop and flushing.

The overstorey had a higher proportion of Group III species than the understorey $(25/93 \ v. 7/92)$. Three of the seven understorey species, which experienced leaf drop, lost their leaves for extended periods; the others replaced their leaves immediately. All but one of the twenty-five overstorey species, which either lost leaves or became leafless, remained leafless or near leafless for an average of six weeks, with a range of two to fourteen weeks.

Leaf drop and reproductive activity coincided in two of the seven understorey species in Group III. Jacaratia dolichaula lost its leaves during the flowering period, which lasted for two months in the pistillate plants and five months in the staminate. The behaviour of this species was unusual since flowering and leaf drop occurred only in the lower half of the crown; the upper portion of the crown remained in leaf. Throughout the extended flowering period numerous tufts of small new leaves could be observed on the branchlets which bore flowers; however, enlargement of these leaves did not occur until after flowering had ceased. This synchronized leaf/flower behaviour may have evolved through facilitation of the location of flowers by pollinators (which are probably nocturnal moths). Simultaneous leafing also allows the species to remain in competition for existing light while flowering for an extended period of time (Baker 1970).

Shedding of leaves synchronously with maturation of fleshy fruits occurred in part in *Tovomotopsis multiflora* and may aid the plant by 'advertising' the presence of fruits to potential dispersal agents. *Aegiphila falcata* became leafless for an extended period (2-4 months) just after the mature fruits were shed. In addition to losing their leaves, trees of this species also shed numerous branchlets, in some cases to such an extent that they appeared dead shortly after fruiting had ceased.

As with the understorey species, leaf fall and sexual reproductive activity coincided partially or completely in many of the overstorey species in Group III (14/25). Seven species lost their leaves at the time of flowering. The most noticeable floral synchronizations were observed in *Castilla elastica*, *Ceiba pentandra* and *Erythrina cochleata*. *Ceiba pentandra* is well known for its correlated leaf fall/flowering behaviour (Baker & Harris 1959; Taylor 1960). *Erythrina cochleata* was similar in its behaviour to *Jacaratia dolichaula* in that during an extended period of flowering (14 weeks) the tree was leafless. Once flowering ceased, production of new leaves occurred almost immediately. Standley (1922) mentioned that leaflessness and flowering often coincide in the genus *Erythrina*.

Nine species lost their leaves during maturation of fruit. Four of these, *Cedrela* odorata, *Ceiba pentandra*, *Cordia alliodora*, and *Luehea seemannii*, had fruits adapted for wind dispersal, and leaflessness at this time probably aided in effective dispersal of their seeds (Lowe 1968). The remaining five species were variously adapted for dispersal. Two produced fleshy disseminules and may benefit from greater prominence of the fruits in the leafless condition.

Richards (1952, p. 193) stated that '. . . most rain-forest trees produce new leaves, not continuously, but in periodic flushes, so that a single shoot bears several "generations" of leaves at the same time'. However, almost two years of continual observation revealed that, at La Selva, continuous leafing (within the limits of observational resolution) was characteristic of 26 (28%) and 37 (40%) of the species in the overstorey and understorey respectively (Table 2). The greater proportion in the understorey is notable.



FIG. 6. Flowering periodicity of overstorey tree species at Wet forest site. All species, continuous line; seasonally flowering species, pecked line.

Flowering activity

Flowering periods of the various species in each storey were examined on a monthly basis. In Figs. 6 and 7, the 'seasonal flowerers' have been divided from the total of 'seasonal' plus 'extended flowerers' to facilitate the viewing of a minor pattern as well as the major one (flowering periods in parentheses in Appendix, Lists 1 and 2, were not included in the compilation). The 'seasonally-flowering' species bloom in one or both of the dry or wet seasons, while the 'extended-flowering' species bloom over two or more consecutive seasons.

Periodicity of overstorey trees

During the first two months of the dry season (February–March) a large number of species bloomed (Fig. 6). After this period, flowering activity of the 'seasonallyflowering' species declined. It then increased in May (beginning of the first wet season) but decreased until it reached the yearly low in November (the small peak in flowering in September represented a second flowering of a limited number of 'dry season flowerers'). When all the overstorey species were considered together, there was an apparent drop in



FIG. 7. Flowering periodicity of understorey tree species at Wet forest site. All species, continuous line; seasonally flowering species, pecked line.

June, but the proportion rose again in July after which it decreased to the yearly low in November. Clearly, the 'extended-flowering' species contributed most of the flowering from July to September in the overstorey.

Periodicity of understorey trees

Three apparent peaks in flowering activity are found when all species are considered together (Fig. 7). The first peak occurred from January (end of second wet season) to March (middle of the first dry season). The 'seasonally-flowering' species also experienced a slight increase in flowering in March. The other two apparent peaks were in June and August–September, respectively. The June high, which coincided with the middle of the first rainy season, was in part due to the 'seasonal flowerers'. After the August–September blooming peak, flowering of all species dropped off sharply until the year's lowest activity was reached in December. It is noteworthy that the contribution of the 'extended-flowering' species is so great that it determines the nature of the overall pattern.

Table 3. Number of Wet forest tree species flowering in dry and wet seasons

	Dry				Wet		Extended	Season	
	I	п	Both	I	II I	Both	flowering*	unknown	Totals
Overstorey	16	5	8	15	6	1	31	11	93
Understorey	13	7	2	7	4	2	45	12	92
Totals Dry: I Dry: II	29 Februar August–	12 y–A Octo	10 pril ober	22	10	3	76 Wet: I Wet: II	23 May–July November–Ja	185 nuary

* Produce flowers over an extended period irrespective of season.

At least two of the flowering peaks in the overstorey appear to be out of phase with two of the understorey peaks. Thus, the June and August-September peaks of flowering in the understorey followed one month after the May and July-August peaks of the overstorey.

Behaviour of 'seasonal' and 'extended' flowerers

'Seasonally-flowering' species of the overstorey averaged 6.6 weeks in flower (± 4.1 S.D.) while 'seasonally-flowering' species of the understorey averaged 6.4 weeks in flower (± 5.2 S.D.). The 'extended-flowering' species of the two storeys also had similar flowering periods: 20.8 ± 14.3 weeks and 25.5 ± 16.5 weeks respectively.

At La Selva, most periodically flowering species appear to be 'programmed' to flower in either one dry or one wet season (Table 3). Highest periods of seasonal flowering, considered separately by storey or pooled, occurred during the first dry and first wet seasons, with similar numbers of species flowering in each season. Approximately the same number of species in both storeys flowered during the second dry and second wet seasons, respectively.

The number of 'seasonally-flowering' species which flowered during both dry or both wet seasons was low, most of them being overstorey species flowering in both dry seasons.

Within both storeys there were species whose flowering extended over two or more consecutive seasons (Table 3). Examples of overstorey 'extended flowerers' included: *Rollinia microsepala* and *Guatteria aeruginosa*. In the understorey, the same flowering behaviour was observed in *Cassia fruticosa* and *Warszewiczia coccinea*. In addition, 16 of 31 'extended flowerers' in the overstorey bloomed in two and occasionally three

separate bursts, irrespective of the season. An almost equal proportion of species (21 of 45) in the understorey behaved in the same manner by flowering in separate periods of the wet and dry seasons. Examples of the former group include: *Genipa caruto* and *Trophis racemosa*; the latter group is represented by *Compsoneura sprucei* and *Vismia latifolia*.

Variation in flowering activity

Two variations were found in a few species in both storeys. The first was that of unsynchronized flowering among individuals of one species (Table 4, and see species designated US in Appendix, Lists 1 and 2). A species having only infrequent deviants was not included in this category. Lack of synchrony was observed in almost equal proportions for both storeys; *Bravaisia integerrima*, *Spondias mombin* and *Virola koschnyi* best exemplified it. *V. koschnyi* was not expected in this group since it is dioe-

Table 4. Proportions of Wet forest tree species showing each of two kinds of deviation in flowering activity

Layer	Unsynchronized flowering	Differences between years
Overstorey Understorey	10/82 (12%) 10/80 (14%)	20/82 (24%) 15/80 (19%)
Totals	20/162 (13%)	35/162 (22%)

cious and depends upon synchronization in flowering for successful pollination. Another form of this variation was observed when a small, but internally synchronized, portion of a population suddenly burst into full or partial flower. *Spondias mombin* was commonly observed behaving in this manner; such flowering rarely resulted in fruit set.

Another kind of deviation in flowering pattern involved a difference in annual flowering intensity (species designated DA in Appendix, Lists 1 and 2) and/or difference in the period of flowering between years (DP in Appendix, Lists 1 and 2). This variation occurred in both storeys (Table 4). *Terminalia oblonga* produced many flowers in 1969 but few in 1970. *Vochysia hondurensis* flowered profusely in March and April 1969 but produced no flowers in 1970. It should be remembered that 1969 was a relatively 'dry' year for La Selva, while 1970 was an extremely 'wet' year (Fig. 2). *Hernandia stenura* in 1969 flowered from August to November but in 1970 from March until mid May. *Casearia arborea* and *Inga* sp. II behaved similarly.

Fruiting activity

Periodicity of overstorey trees

Major periods of activity occurred in September and October respectively in the overstorey and understorey, i.e. in the second dry season (Figs. 8 and 9). Periods of mature fruit noted in parentheses in Appendix, Lists 1 and 2, were not included in these compilations. In the overstorey the fruiting periodicity of 'seasonal fruiters' corresponded closely to that of all species taken together (Fig. 8). However, in the understorey the 'seasonal fruiters' exhibited a pattern that departed strikingly from the pattern for the storey as a whole (Fig. 9). The slight rise in activity in September of 'seasonal-fruiting' species did not appear to contribute significantly to the overall understorey pattern, which was made up mostly of 'extended-fruiting' species. During no month was the



FIG. 8. Fruiting periodicity of overstorey tree species at Wet forest site. All species, continuous line; seasonally fruiting species, pecked line.

number of species in fruit in both storeys less than 37 (the minimum was in June); a continual source of food was thereby provided to resident frugivorous animals.

Behaviour of 'seasonal' and 'extended' fruiters

Many tree species produced fruits over an extended period, spanning portions of two or more consecutive seasons. Extended fruiting occurred more commonly in the understorey (54 of 92 species) as compared with the overstorey (31 of 93 species) (Table 5). The difference is significant (P < 0.05). Within this 'extended-fruiting' group there were also a few species that matured fruit discontinuously in two (rarely three) disjunct periods. In the overstorey, Virola koschnyi and Guarea longipetiola produced fruit during two seasons; while in the understorey Aegiphila falcata also fruited twice. Another understorey tree, Capparis pittieri, matured its fruit during three separate periods.



FIG. 9. Fruiting periodicity of understorey tree species at Wet forest site. All species, continuous line; seasonally fruiting species, pecked line.

'Seasonally-fruiting' species matured their fruit in either a wet or a dry season. Almost twice the number of 'seasonal fruiters' matured fruit in the second dry season as compared with any other season (Table 5). Differences in fruit types were noted. Over 90% of the tree species that fruited in the study period at La Selva had fleshy fruits (67 of the overstorey species and 80 in the understorey). Of the 14 non-fleshy fruited species, 12 (10 of which were in the overstorey) were adapted for wind dispersal. Examples of these include: *Ceiba pentandra, Luehea seemannii* and *Pterocarpus officinalis*. The remaining two species, *Apeiba membranacea* and *Pithecolobium longifolium*, produced fruits which had no apparent adaptation for dispersal. Information on seed ecology and related matters will be published later.

A peculiar habit, which deserves more attention, was observed in some of the species having fleshy fruits. Three species, *Meliosma* sp., *Pouteria lucentifolia* and *Quararibea* sp., retained fruits on the parent plant, in what appeared to be a mature condition, for several months. During this period the fruits generally disappeared at the rate of a few per week until all were gone. This retention of mature fruits, in an attractive condition, was also observed in a few shrubs. The behaviour may suggest a form of 'insurance' for dispersal by allowing time for the dispersing animal agents to deal with them.

Table	5.	Distribution	by	season	of	^c species	fruiting	periodicall	v i	in Wet	forest
			~		~			4	-		

	Dry season		Wet season			Extended			
	I	II	Both	Ι	II	Both	fruiters*	Unknown	Totals
Overstorey	10	18	1	9	7	1	31	16	93
Understorey	5	9	1	5	9	1	54	8	92
Totals	15	27	2	14	16	2	85	24	185

* Produce fruit over an extended period irrespective of season.

RESULTS: DRY FOREST SITE

Leafing activity

A high percentage of the tree species lost their leaves during the long dry season. At the onset of the first rains (May-June) most tree species flushed large quantities of new leaves. Leaf production continued into July, by which time all species were in full leaf.

Leaf fall periodicity

Leaf fall began as early as October, but the main period was from January to April, with the peak in March (Fig. 10). During the year, 85 of the 113 species partially or completely lost their leaves. Nineteen species (17%) were evergreen, e.g. Guarea luxii, Muntingia calabura, Ocotea veraguensis and Simarouba glauca; most of them were found in the riparian community where the deciduous habit was never obvious. Trees of many riparian species dropped all their leaves at one time but in all of these cases new leaves appeared simultaneously. Information on the behaviour of nine species (5%) was inadequate to allow any conclusions.

One species, *Achras zapota*, appeared to be synchronized in leaf drop and flowering. Prior to flowering in May–June, leaves in the upper two-thirds of the canopy were shed. Shortly thereafter, a brief period of flowering ensued which, in turn, was followed by the almost immediate production of new leaves over the entire tree.

Leaf flushing periodicity

The most intense leaf flushing occurred from late April to June, with the peak in May (Fig. 10). The relatively high period of activity in April took place just prior to the onset of the rains (Fig. 3) and could have been the result of occasional rain showers. However, in 1970, when showers fell in early April in some parts of Comelco, several species were observed putting out new leaves in the unwetted areas of the property. Although leaf expansion began, it stopped until full expansion took place with the start of the first heavy rains of the year.

One Dry forest species, *Lysiloma seemannii*, behaved unusually in that production of new leaves did not occur until one month into the rainy season. Prior to flushing the species was leafless. When the species was almost fully in leaf, it flowered profusely.

Although the main leaf flushing period was over by July, production of a few new leaves by each species generally continued into late August. After this time there was little noticeable leaf activity until the beginning of the long dry season. It appeared, therefore, that some form of apical dormancy was present.



FIG. 10. Leaf fall and leaf flushing periodicities of Dry forest tree species. Leaf fall (all species), pecked line; leaf flushing (all species), continuous line.

Minor patterns of leafing behaviour

Several tree species at Comelco also flushed many new leaves from January to March, with January having, by a slight margin, the highest level of activity. Most of these were found in the riparian community, where thirteen of the twenty characteristic species flushed at this time. These included *Anacardium excelsum*, *Hymenaea courbaril*, and *Rheedia edulis* in January, and *Coccoloba padiformis* and *Pithecolobium longifolium* in February.

A few species of the Dry and Moist Deciduous forest communities, as well as derived savanna and second growth communities were in full leaf throughout most of both seasons. Species of the first two communities included *Clusia rosea*, *Styrax argenteus* var. *argenteus*, *Schoepfia schreberi* and *Albizia longepedata*. The last species lost its

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leaves only in January, after which time it leafed out and remained in full leaf for the rest of the year.

Individual trees of *Caesalpinia eriostachys* remained nearly fully leafed throughout the year wherever they occurred on moist soils. On these wetter sites, the trees generally flushed new leaves more than once during the long dry season. On drier soils, trees lost leaves for a large portion of the dry season.

In derived savanna, *Byrsonima crassifolia* and *Simarouba glauca* kept their leaves throughout the year. Both of these species flushed large numbers of new leaves in mid-dry season. Two other species, *Cecropia peltata* and *Muntingia calabura*, both second growth species, were also in leaf during the entire year.



FIG. 11. Flowering periodicity of Dry forest tree species (April 1969–July 1970). All species, continuous line; seasonally flowering species, pecked line.

Flowering activity

Flowering of most species is restricted to a particular season, with the long dry season having the greatest number of species in flower. Flowering activity can be divided according to four climatic seasons (Fig. 3), but it is becoming apparent, after more than five years of study, that this division may be greater than is necessary to reveal flowering patterns in the area around Comelco. Observations of vegetational responses suggest that, operationally, there are only two seasons in the Dry forest site; the long dry period from mid November to late May and the long wet period from late May to mid November. Therefore, most of the remaining flower and fruit phenology data have been expressed in terms of only these two seasons.

Periodicity of Dry forest trees

The 'seasonally-flowering' species followed essentially the same patterns as did the total species group in 1969–70 (Fig. 11); flowering periods in parenthesis in Appendix, List 3, were not included in the compilation. Although the dry season begins in November, appreciable flowering in the tree storey did not begin until January. Within the major flowering period of the dry season (January–April) there was a minor cessation in flowering activity in mid March that lasted for approximately three weeks (based on a compilation of two week flowering periods from January–April). It was also observed in 1971 and 1972; in these years it occurred earlier in the dry season. After mid April, flowering activity dropped off sharply.

At the onset of the rainy season in May-June, there was a pronounced but brief

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period of flowering of slightly more than two weeks. Several tree species responded to the heavy rains by opening their flowers within a few days. This sensitivity became evident when, in early April 1970, localized heavy showers in two study subsites resulted in partial to full flowering of most individuals of *Casearia aculeata, Eugenia salamensis* var. *hiraeifolia, Guarea luxii, Guettarda ?macrosperma* and *Rehdera trinervis*. In a third subsite, which received no precipitation in April, these species did not flower until shortly after the first rains of late May. During these late May rains, the same individuals of the first two subsites, which had flowered in April, again produced a nearly full set of flowers. It was noteworthy that the common 'wet season-flowering' species bloomed predominantly during late May–June of the rainy season (Table 6). After the June peak in flowering, activity dropped off sharply and continued to decline rapidly until November.

Behaviour of 'seasonal' and 'extended' flowerers

Of the 113 tree species under observation at Comelco, 107 species flowered at some time during the period from April to July 1970. Fifty-nine species flowered in the long dry season, 35 in the wet season, and 13 species during an extended period which included portions of both seasons (Table 6).

Mean flowering time for 'dry season-flowering' species was 5.6 weeks (± 2.8 S.D.). Almost all Dry forest species showed good intrapopulation synchronization. Some species, *Tabebuia neochrysantha* and *T. palmeri*, had extremely short periods of flowering, with each finishing its flowering in less than a week. In contrast, *Swietenia humilis*, *Byrsonima crassifolia*, and *Caesalpinia eriostachys* flowered for more than two months during the same season.

The 'dry season-flowering' species were well represented by common, occasional and rare species in all communities, with a few more species in the common group (Table 6). Placing of species in frequency groups in Table 6 was based upon relative abundance of each species encountered in the randomly laid out transects together with a general knowledge of abundance of tree species throughout all the Dry forest communities. A species was considered rare if it was only rarely present in one or more communities or if it was restricted to a micro-habitat within a particular community (e.g. extremely shallow, rocky soil in the Dry Deciduous forest or unusually moist sites within the Dry Deciduous or Moist Deciduous forests). Sometimes, therefore, a 'rare' species may have been relatively common within a particular highly restricted habitat. Almost half of the 16 rare species that flowered in the dry season appeared to be habitat-restricted.

Examples of common species included Anacardium excelsum and Curatella americana; Miconia argentea and Pithecolobium saman represented the occasional category. Rheedia edulis and Lonchocarpus eriocarinalis were considered rare, the last-named being also habitat-restricted.

The majority of 'dry season-flowering' species displayed conspicuous masses of flowers. The nearly leafless nature of the forest in the dry season added to their conspicuousness. There was an almost uninterrupted within-season progression of flowering species, encompassing 59 species in the one long dry season.

Mean flowering time for 'wet season flowerers' was 5.5 weeks (\pm 5.0 S.D.) and was closely comparable to that of species flowering in the dry season. As in the dry season, there were a few species that flowered over very short periods, e.g. *Psidium sartorianum*, in which flowering was over in less than one week, while others had relatively lengthy periods of flowering, e.g. *Apeiba tibourbou* and *Chlorophora tinctoria* with periods of 28 and 16 weeks respectively.

In contrast to species flowering in the dry season (Table 6), the majority of species flowering in the wet season were classified as 'rare'. As with the dry season species, half of the wet season rare species appeared to be habitat-restricted. Examples of common species included *Apeiba tibourbou* and *Chomelia spinosa*; *Chlorophora tinctoria* and *Psidium sartorianum* represented the occasional species group. *Alvaradoa amorphoides* and *Cassia skinneri* were classified as rare; the former was considered habitat-restricted.

Flowering trees were less noticeable during the wet season than were those of the dry season for several reasons; smaller flower size, paler colours, fewer species in flower, the more 'closed' nature of the forest due to the leafed-out condition of all species, and relative rarity of the species themselves were the most important factors. Other factors contributing to inconspicuousness were habitat-restriction in half the rare species and an unequal within-season distribution of flowering species, with most activity occurring at the onset of the rainy period.

Table 6. Season of flowering related to abundance of Dry forest tree species

	Number of	Abundance of flowering species				
	species flowering	Common	Occasional	Rare		
Dry season	59	26	17	16		
Wet season	35	10	5	20		
Extended	13	3	5	5		
Totals	107	39	27	41		

The 'extended-flowering' species had a mean period of 24.7 weeks in flower (± 11.6 S.D.). Differences between the mean of the 'extended-flowering' species and each of the means for the 'wet-' and 'dry-season-flowering' species were significant (P < 0.01).

Owing to the small number of species and their relatively infrequent occurrence, the 'extended-flowering' group did not add significantly to the conspicuousness of flowering in either season. All 'extended-flowering' species were in full leaf during their flowering periods.

Deviations from the main flowering patterns

1. Unsynchronized flowering. Only two species displayed unsynchronized activity in which some individuals flowered out of phase with other members of the same species. *Sterculia apetala* flowered primarily in March. However, flowering among some individuals also occurred in February and September. Flowering of a few individuals in November 1969 and January 1970 was also recorded. *Crescentia alata* behaved in a similar but less extreme manner, with most of its flowering occurring in the wet season. During the dry season occasional individuals produced large numbers of flowers. Some individuals seemed to flower continuously throughout the year.

2. Differences year by year. Twelve tree species in Comelco showed distinct yearly differences in flowering activity from 1969 to 1972. In some, flowering in one year was followed in the second year by no appreciable flowering. In 1969, marked individuals of *Ceiba pentandra*, *Dalbergia retusa*, and *Piscidia carthagenensis* flowered and produced sizeable fruit crops. However, no flowering activity was observed in 1970 in any of these marked trees (although in some sites of Comelco unmarked individuals of the latter two species flowered and fruited in 1970). Marked individuals of *Dalbergia retusa* and *Piscidia carthagenensis* flowered in 1972. With *Ceiba*

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pentandra, however, no marked individuals flowered in 1970, 1971 or 1972. Baker (unpublished) observed a similar behaviour for *C. pentandra* in Africa (see Baker & Harris 1959). Marked individuals of a fourth species, *Astronium graveolens*, produced no flowers in 1970, but flowered in 1971. In 1972, flowering in some of the same individuals was observed. Other species which did not appear to flower every year included *Andira inermis, Lonchocarpus eriocarinalis, Myrospermum frutescens, Platymiscium pleiostachyum, Pterocarpus rohrii*, and *Tabebuia palmeri*.

The second form of year-to-year variation, in this case involving an annual shift in flowering period of one or more months, was noted in *Licania arborea*, *Tabebuia palmeri*, *T. neochrysantha*, and *Genipa caruto*. In 1969, *Licania arborea* flowered in December. The next flowering period occurred in January of 1971. This late flowering was interesting since, throughout the dry forest, flowering activity in the 1971 dry season was generally



FIG. 12. Fruiting periodicity of Dry forest tree species (all species).

advanced over that of the previous year's dry season. *Tabebuia palmeri* and *T. neo-chrysantha* each flowered only once in the dry season of 1970; in 1971 both species flowered with equal intensity on three separate occasions in the dry season. In 1969, *Genipa caruto* flowered in June, and in 1970, it flowered twice, once in late May to early June and again in late July. Wolf (1970), working at the Granja Experimental Jiménez study site (about 40 km away), recorded *G. caruto* flowering mostly in June and July with lesser activity in February and April–May of 1967.

3. Species flowering more than once during year. In any one species each flowering observed produced roughly equal numbers of flowers. *Tabebuia palmeri* and *T. neo-chrysantha* best exemplified this behaviour. In addition, *Laetia thamnia* flowered three times in 1970 and *Pithecolobium dulce* twice in 1971. All of these species flowered in the dry season. *Swietenia humilis* flowered from February to early April in 1970 and again in July of the same year. *S. humilis* was rather peculiar in that most individuals which flowered in the dry season did not flower a second time in the wet period.

Fruiting activity

Most Dry forest tree species were seasonal in their production of mature fruits. Of 113 species studied, 104 produced mature fruit.

Periodicity of all species

A single large peak in fruiting activity occurred in April (Fig. 12); periods of mature fruit shown in parenthesis in the Appendix, List 3, were not included in this compilation. During this peak period 41 species, representing nearly equal proportions of a wide range of fruit types, produced mature fruits. Examples include *Anacardium excelsum* (fleshy), *Bombacopsis quinata* (wind-dispersed) and *Calycophyllum candidissimum* (no apparent dispersal adaptation). The number of species in fruit decreased to 22 in May; twelve of these began fruiting in April.

From June to November the production of mature fruits remained low, but relatively constant, with seven to thirteen species in fruit during any month. After November, the number of fruiting species rose to 17 and remained at that level from December to February.

Relationship of flowering and fruiting periods

When periods of flowering are compared with the respective periods of fruiting for each species, an interesting pattern of dry season fruiting emerges. Regardless of flowering season, most species (75) matured their fruits in the dry season (Table 7). Of

 Table 7. Comparison of flowering season and fruiting season for Dry forest

 tree species

Flowering season	Number of species in flower	Number Dry season	r of specie Wet season	es maturing Extended season	fruit in Un- known
Dry season	59	48	7*	2	2
Wet season	35	20*	10†	1	4
Extended season	13	7	2	4†	0
Totals	107	75	19	7	6

* Trees matured fruits in the season which directly followed their flowering season.

† Trees matured fruits during the same season in which they flowered.

Table 8.	'Dry season fruiters	' which flowered	during the	e previous a	lry season
	a	t the Dry forest	site		

Species	Month(s) in flower	Month(s) in mature fruit
Albizia caribaea	March	March
Bursera simarouba	April–mid-May	April
Cassia grandis	mid-FebMarch	Dry*
Dalbergia retusa	mid-March-mid-April	Dry*
Diospyros nicaraguensis	May	mid-NovFeb.
Enterolobium cyclocarpum	April	April
Godmania aesculifolia	April-May	DecFeb.
Hemiangium excelsum	March-April	FebMarch
Hymenaea courbaril	mid-March-mid-April	DecJan.
Lonchocarpus costaricensis	mid-March-mid-April	Dry*
L. eriocarinalis	April	mid-NovDec.
Pithecolobium saman	April	March
?Stillingia sp.	April	Dry*
Swietenia humilis	Feb.–March, July	Jan.

* Fruit was shed at some period during the dry season, and information to date suggests that fruit drop is irregular.

the 48 'dry season flowerers' whose flowers *and* fruits were matured in the dry season, 34 matured their fruits during the season in which they flowered; the other 14 species required from 8 to 12 months to complete maturation and ripened their fruits in the dry season of the following year (Table 8). Only two of the 'wet season flowering' species required more than eight months to produce mature fruit; *Genipa caruto* and *Guarea luxii* both needed 10 months.

Fruit-type

The fruit-types of the species fruiting in each season are shown in Table 9. Taken collectively, c. 50% of the species had fleshy fruits, c. 30% were adapted for wind dispersal, and c. 20% were neither fleshy nor wind-adapted. These fruit-types will be considered in detail in a subsequent paper.

The relative abundance of fruit-types depended upon the season. In the dry season, the fleshy habit (27 species) was almost as frequently encountered as the wind-adapted

Table 9. Season of fruit maturity related to fruit-type for Dry forest tree species

	Number of species in mature fruit	Fleshy	Fruit type Wind- adapted	s Miscellaneous
Dry season	75	27	32	16
Wet season	21	19	0	2
Extended	8	7	0	1
Totals	104	53	32	19

type (32 species); species having other kinds of dispersal adaptation (16) were mostly found at this time. In the wet season, 19 out of 21 fruiting species were of the fleshy fruit-type. Fleshy fruits were also commonest in the 'extended-fruiting' species group (7/8 species). High relative abundance of wind-dispersed types in the dry season was important since fruiting coincided with the period of Dry forest leaflessness and the period when the winds of Guanacaste Province blew with the greatest intensity and frequency.

April peak

Forty-one species were seen in fruit in April. Thirty-four of the 59 'dry season flowering' species fruited during the season in which they flowered. Regardless of when they flowered in the period of December to March, 27 of the 34 species produced mature fruit in April. The fruits of the other 14 species fruiting in April resulted from species flowering during the wet season, during the previous dry season or during portions of both seasons.

The 25 'dry season flowering' species that did not mature fruits in April (or in one of the other dry season months) consisted of two groups. The first (11 species) fruited during the wet season, during portions of both seasons, or did not fruit. The second group (14 species) flowered in late March, April or early May and did not mature their fruits until the dry period of the following year (Table 8). It seems possible that these species, because of their late flowering periods, have not the capacity to mature their fruits quickly enough to coincide with the April peak, but rather have evolved the capacity for their fruits to remain immature until the following dry season.

The reasons for the concentration of fruiting species in April are not entirely clear.

There are at least two important questions relating to the seemingly pivotal nature of the April fruiting peak and the great difference in species fruiting in the dry season rather than the wet season (Table 9). Why do relatively few species fruit in the months immediately after April? Also, why do fourteen late 'dry season flowerers' retain immature fruit until the following dry period?

April is probably the latest possible time of the year when disseminules can still be dispersed effectively before the rains begin in May. After that, effective dispersal would be reduced by the rains and by the fully expanded leaves of the forest canopy.

In addition, limited data suggest that the 'wet season fruiters' have evolved a type of dormancy mechanism that tends to prevent germination of their seed during the same wet period. Of 57 'dry season-fruiting' species on which germination trials were attempted, 47 showed some quick germination and in all but two cases 50% or more of the seeds had germinated in less than 70 days. Of six 'wet season-fruiting' species, three showed some germination. However, in all three species (i.e. *Casearia aculeata, Eugenia salamensis* var. *hiraeifolia* and *Spondias mombin*) the time necessary to germinate 50% of the seeds was approximately 150 days. Such dormancy tends to ensure that germination will be synchronized seasonally among the species so as to allow for rapid root establishment at the onset of the yearly rains. Seed germinating later would not have time to develop a root system adequate to carry the seedlings through the short dry season (July–August) and the succeeding long dry season (late November–May).

RESULTS: COMPARISON OF WET AND DRY FOREST PATTERNS Leaf drop and leaf production

Striking leaf changes take place in a greater proportion of species (75%) in the Dry forest than in the Wet forest (17%). The length of the leafless period for individual species and for the ecosystem as a whole is also significantly longer in the Dry forest. This is the case even though substantial leaf drop does not usually begin until about six weeks into the dry season in the Dry forest but begins just prior to the onset of the first dry season in the Wet forest.

Leaf flushing is also different in the two areas. Wet forest species produced most of their leaves during the most severe dry season (February-April), while Dry forest species flushed predominantly during the beginning of the wet season (May-June). At the Wet forest site, a few species (10) produced large numbers of new leaves during each dry season; nine Dry forest species flushed new leaves during dry and wet seasons. It was also noteworthy that a sizeable number of Wet forest species produced leaves at a low but constant rate throughout the year while, in the Dry forest, all but *Muntingia calabura* displayed seasonal leaf flushing behaviour.

Flowering

At the Wet forest site, most 'seasonally-flowering' species bloomed during the first dry and first wet seasons of the year (February–July). Species in flower were reduced almost to half during the second dry and second wet seasons of the year (August–January). Similarly, slightly more than half of the flowering at the Dry forest site occurred in the long dry season (November–May) with only about one-third of the species flowering during the long wet season (June–October).

Species that produced flowers irrespective of season were more commonly observed

at the Wet forest site. At this site, approximately 12% of the marked species did not flower during the observation period; at the Dry forest site 5% did not produce flowers.

Inconsistency in flowering time was observed in a small proportion of the species of both forests. This type of variation was more pronounced at the Wet forest site. Year-to-year differences were observed in about the same proportion of cases in each forest. Flowering in disjunct periods was observed in both forests. However, at the Wet forest site this activity often occurred irrespective of season, while in the Dry forest almost all of these flowerings occurred within one season.

Ten species flowered exclusively in both dry seasons at the Wet forest site while only *Swietenia humilis* at the Dry forest site produced flowers in both dry seasons. However, the second dry season at the Wet forest site is generally of longer duration (although less severe) than the second dry season at the Dry forest site.

Lengths of blooming periods were remarkably similar for the 'seasonally-flowering' species in both forests (average c. 5–6 weeks). Mean flowering periods for species with extended blooming periods in both forests were also similar (21–25 weeks).

Fruiting

At the Wet forest site, although most fruiting occurred during the second, shorter dry season (August-October), it was possible to find at least 37 species bearing mature fruit in any month of the year. At the Dry forest site a pronounced peak in fruiting activity occurred in April during the long dry season. At this site some fruiting could be found in every month, but the species with mature fruit declined to a low level in the period August to October.

Leafing activity during peak fruiting periods in the two forests differed markedly. At the Wet forest site, all trees were in full leaf in September and October (peak fruiting periods in the overstorey and understorey respectively), while at the Dry forest site most trees were leafless during the April fruiting peak.

At the Wet forest site, only 12 species (7%) had seeds or fruits adapted for wind dispersal, while at the Dry forest site 33 (32%) possessed wind-adapted disseminules. During most months in the Wet forest, one to five species with wind-adapted fruits or seeds could be found; however, in the Dry forest, this type of dispersal system was present only during the long dry season.

Comparison of Wet forest site species and riparian species of the Dry forest site

Riparian species generally followed the same pattern as those in other communities at the Dry forest site in respect to flowering and fruiting patterns, but they showed distinct parallels with the Wet forest species with regard to leaf fall and development. Leaffall activity at the Wet forest site occurred primarily during the last month of the second wet season and during all of the first dry season (January–April). At the Dry forest site at the riparian community, most deciduous species lost their leaves during the middle part of the long dry season (January–April); the flushing of many new leaves also occurred then, only a little earlier than at the Wet forest site. Flushing of new leaves at this time in the riparian community was in contrast to the general absence of flushing in other communities of the Dry forest.

Vicarious species of the Dry and Wet forests

Twenty-seven genera are known from both forest sites; between one and five species per genus are involved. Eight of these genera occurred in the riparian community at the Dry forest site (Brosimum, Guarea, Licania, Ocotea, Pouteria, Sloanea, Swartzia, and Zanthoxylum). For five of these genera the species involved showed comparable seasonal patterns of leaf change with their counterparts in the undisturbed dry ground forest of the Wet forest site. Similar patterns of leaf change within the pairs of vicarious species were recognized in only five of the remaining 19 genera: Casearia, Cecropia, Loncho-carpus, Pterocarpus, and Spondias. The remaining pairs showed patterns of leaf activity that generally conformed to patterns characteristic of the respective forests.

Of the 27 genera, 11 contained vicarious species whose yearly patterns of flowering were essentially the same whether as 'seasonally-flowering' species (whose seasons of bloom were the same) or 'extended-flowering' species (which flowered during portions of at least one wet and one dry season). Seasonal differences in flowering occurred in *Cordia, Guarea, Laetia, Luehea, and Pithecolobium.* In all except *Laetia, more than one species per forest was involved in the comparison.* It is of particular interest that genera containing more than one species at a site were made up of species which had different flowering times. For example, in *Guarea* at the Wet forest site, two species flowered in the first dry season during separate periods; a third species flowered in the first wet season, and a fourth species flowered on three separate occasions during three different seasons.

Five of the 27 genera contained vicarious species whose seasonal fruiting patterns were similar. Differences observed in the remaining genera stemmed largely from those species in the Dry forest which tended towards the April fruiting peak and those in the Wet forest which tended to fruit at the September–October peak. In both sites, fruiting periods of species in the same genus were usually separated in time or were extended over long periods.

Species in common between the Wet and Dry forest sites

Eleven tree species were found to be common to the two forest sites. Also, three other species, *Casearia nitida, Hamelia patens*, and *Hirtella racemosa*, were found as trees in the Wet forest and as shrubs in the Dry forest. Leafing activity in eight of the eleven tree species was essentially the same in the two sites. In one of the three exceptions, *Genipa caruto*, the Wet forest representative was evergreen throughout the year with one major leaf flush in April while, in the Dry forest, it was observed dropping leaves from January through April, followed by a flush of new leaves in May–June. The other two exceptions, *Casearia arborea* and *Ochroma pyramidale*, produced a few new leaves each month without noticeable leaf drop in the Wet forest but in the Dry forest these species experienced leaf drop in late dry season (April–May) and flushing at the onset of the rainy season (late May–June).

Seasons of flowering were similar in five of the eleven species: Andira inermis, Cedrela odorata, Cordia alliodora, Hura crepitans, and Rheedia edulis. Two of the species, Ceiba pentandra and Ochroma pyramidale, flowered during the same months; however, the respective events occurred in different seasons (see Figs. 2 and 3). Casearia arborea, Genipa caruto, and Spondias mombin differed markedly in flowering periodicity between the two sites. In the remaining species, Pithecolobium longifolium, additional data are needed before periodicity behaviour can be evaluated.

Six of the eleven flowered either for longer periods or during two periods in the Wet forest as compared to the Dry forest. For example, *Cedrela odorata* flowered for eight weeks in the Wet forest and for four weeks in the Dry forest. *Spondias mombin*, in Wet forest, consistently flowered for longer periods than its counterpart in the Dry

forest. In contrast, *Ochroma pyramidale* flowered for four weeks in the Wet forest and eight weeks in the Dry forest.

Comparable information on periods of fruit maturation are available for eight species in common between sites. *Ceiba pentandra, Cordia alliodora, and Ochroma pyramidale* matured fruit in the same season at both sites. *Casearia arborea, Cedrela odorata, and Spondias mombin* differed only slightly in their months (and consequently seasons) of mature fruit production. *Genipa caruto* and *Hura crepitans* had different patterns. In the Wet forest, *Genipa caruto* shed its fruits in August, while in the Dry forest this happened in April and May. *Hura crepitans* shed fruit in February in the Wet forest but had two periods of fruit drop in the Dry forest, one in August and one in November.

GENERAL DISCUSSION

Tree periodicity patterns provide insight into seasonal organization of floral and fruitseed resources (and into spatial organization in the case of the two storeys of the Wet forest). Frankie, Baker & Opler (1974) mention several ways of breaking down these patterns further for analyses at finer levels of organization within the respective communities of each ecosystem. They also suggest how these patterns may provide clues as to which animals interact with them for the food resources they provide.

Major patterns of leaf flushing are informative since numerous phytophagous organisms must be synchronized in their life cycles with the succulent leaf resources that become available during peak periods of leafing. The magnitude of this large and diverse food resource is exemplified in all but the riparian community of the Dry forest (where almost all tree species come into full new leaf within a few weeks after the onset of the long wet season). Conversely, major periods of leaf fall must be important to the dynamics of litter organisms that occur in both forests.

Many phenological patterns observed in both forest sites fit well with the seasonal cycle of climatic conditions. However, some patterns may be importantly influenced by biotic as well as by abiotic factors.

Correspondence with seasonal events

Correlation of phenological activity with seasonally occurring events is best exemplified by the patterns of leaf fall and leaf flushing in both forests. The period of greatest leaf fall corresponded with the relatively xeric conditions of the first long dry season at both sites. Other investigators, working in a variety of tropical forest-types, have also observed maximum leaf fall during the driest part of the year; e.g. J. R. Baker & I. Baker (1936) in the New Hebrides, Beard (1946) in Trinidad, Holttum (1931) in Singapore, Madge (1965) and Hopkins (1966) in Nigeria, and Taylor (1960) in Ghana. Amount and rate of leaf drop varied with the intensity of the dry season. This relationship was especially noticeable in the Wet forest site where, during the more severe dry season of 1969, the forest floor was covered with 5 to 10 cm of dry leaf litter, a condition which is rarely observed in Rain forests. Beard (1944) mentions that degree of leaf fall varied similarly with intensity of the dry season in Trinidad. The relationship with available moisture was also noticed when comparing different communities at the Dry forest site; tree species in the Dry Deciduous community, e.g. *Caesalpinia eriostachys*, generally lost leaves in the dry season at a faster rate than those of the Moist Deciduous community.

The production of large quantities of new leaves corresponded with major seasonal

events in both forests. At the Wet forest site most leaf flushing occurred during the (more severe) first dry season, while at the Dry forest site a major period of leaf production ensued at the onset of first wet season rains.

A careful examination of leafing activity in each forest revealed that leaf expansion started just prior to the beginning of the respective seasons in which major flushing periods occurred. Thus, at the Wet forest site leaf expansion began in a number of species in January (the last month of the second wet season), with maximum flushing in the subsequent dry season. At the Dry forest site the first signs of leaf expansion in several species occurred during late April and the first half of May (end of the long dry season). This finding parallels that of Njoku (1963), working with ten Rain forest tree species in the Botanical Garden at Ibadan, Nigeria.

At the Dry forest site, new leaves were noticed on most trees in April (one month prior to the start of the first wet season); this is in keeping with the findings of previous studies in tropical Dry forests around the world; e.g. Boaler (1966) and Jeffers & Boaler (1966) in Tanzania, Champion (1936) in India and Burma, Coster (1923) in Java, Daubenmire (1972) in Costa Rica, Hopkins (1970a) in Nigeria, Rawitscher (1948) in Brazil, Webb (1959) in Australia, and Wright (1905) in Ceylon. Under experimental conditions, Lawton & Akpan (1968) demonstrated that this occurred with *Plumeria acuminata* at Ibadan, Nigeria. Photoperiodic variation may be the controlling factor (Njoku 1963).

Cessation of leaf flushing at the Dry forest site during the second wet season, when conditions seemed to be favourable for growth, may also be influenced by light, in part. Njoku (1963) and Hopkins (1971a,b) made observations on this apical dormancy during the wet season in Nigeria and, in an experimental study, Njoku (1964) demonstrated that in one species, *Hildegardia barteri* (Sterculiaceae), the onset of apical dormancy is influenced by small changes in day length (decreasing daylight hours). Hopkins (1970a) suggested that the most likely factor controlling extension growth was photoperiod but that moisture often exerted a limiting effect; he also cautioned that the factors controlling growth may not be the same for all species.

In both forests of this study, synchronization of flowering with particular seasons by many species appeared to be under the control of prevailing climatic conditions. In the Wet forest, relatively large numbers of species were recorded in flower during the first dry and first wet seasons of the year; lesser numbers were observed in flower during the second dry and second wet seasons. This pattern may provide some support for the suggestion advanced by Holttum (1953), Janzen (1967), and Lawton & Akpan (1968), that sequences of dryness and wetness are important in triggering the flowering response. The habit of flowering with a regular periodicity has been commonly observed in Rain forest trees (Ashton 1969; Bews 1927; Croat 1969; Holttum 1953; Medway 1972; Rees 1964; Richards 1952). Observations by Medway (1972) in his 10-year study of a Tropical Rain forest in Malaya are important since they reveal that, in addition to the seasonally recurrent floral activity displayed by several tree species, the forest community as a whole exhibited a marked seasonal cycle of flowering.

Of interest is the general observation made by several investigators that most Wet forest flowering occurs chiefly during periods of dry weather; e.g. Aubréville (1938) in West Africa, Holttum (1953) in Singapore, Njoku (1963) in Nigeria, Schimper (1903) in Java, and Spruce (1908) and Ducke & Black (1953) in Brazil. The pattern at the Wet forest site was different. There, when the periodicities of all species are considered together, a relatively level abundance of flowering activity results (except for low values in the wet months of November and December). At the Dry forest site, the long dry season brings almost twice as many 'seasonallyflowering' species into bloom as the wet season (cf. Janzen 1967; Fournier & Salas 1966). Investigators working in tropical Dry forests elsewhere in the world have also observed a predominance of dry season flowering, e.g. Airy Shaw (1947) in West Africa, Boaler (1966) in Tanzania, Ducke & Black (1953) in Brazil, and Snow (1962) in Trinidad.

Although moisture-related factors may play the biggest role in controlling flowering in tropical trees, African studies by Njoku (1958, 1963) and Lawton & Akpan (1968) suggest that a change in photoperiod may be an important stimulus in triggering flowering. Njoku (1958) demonstrated that a difference of 15 minutes in photoperiod at Ibadan (latitude 7° 26' N) is sufficient to initiate the flowering process in many herbs and shrubs. In his 1958 and 1963 papers, Njoku suggests that these small photoperiodic changes may also trigger flowering in trees.

The peak in mature fruit production at the Wet forest site corresponds strikingly with the second dry season but no functional correlation with potentially influential abiotic factors in the period spanning the peak is apparent. The temperature and drying power of the air are relatively constant. Although rainfall differences prior to and just after the peak are obvious, there is little reason to suspect that this precipitation pattern is meaningful for fruit development, since a similar pattern (of greater intensity) occurs during the first dry season with no resulting increase in fruiting. It is also curious that there was a month difference in peak fruiting between the two storeys, suggesting that climatic factors are not the only ones involved. If they were, the peaks might be expected to correspond in time as they did for leaf fall and leaf flushing.

Some of the possible factors influencing the fruiting pattern at the Dry forest site have already been discussed (p. 902) but, once again, factors other than abiotic ones may also be involved.

Combined influences of biotic and abiotic factors

Several flowering and fruiting patterns suggest that animal-plant interactions may have a subtle but important influence. Flowering patterns that may be influenced by pollinating animals were observed in both forests. The 59 'dry season-flowering' species of the Dry forest bloomed in a sequential manner through this season with minimal overlap of flowering period recorded among the species. In both forests, the blooming periods of congeneric species did not overlap substantially. In this manner, these species may be avoiding competition for the 'services' of like pollen vectors. General considerations of competition for pollinators by plants have been published recently by Frankie, Baker & Opler (1974), Heinrich & Raven (1972), Hocking (1968), and Levin & Anderson (1970).

The importance of pollen vectors in the reproduction of tropical trees is emphasized by a recent survey of breeding systems of tree species in the Dry forest region around the Dry forest site. Bawa (1974) has found that a high proportion of tree species are selfincompatible or dioecious. Consequently, since most of these species are obligated to outcross, and since wind pollination in the tropics is rare (Baker 1959; Whitehead 1969), they are dependent upon animals for effective pollen transfer.

In both the Wet and Dry forests of Costa Rica certain tree species did not flower on an annual basis. This phenomenon in tropical forest trees has been well documented in other geographical areas, e.g. Ashton (1969) in south-east Asia, Ducke & Black (1953) in Brazil, Fedorov (1966) in tropical Asia, Holttum (1953) in Singapore, Janzen (1970) in Costa Rica, Landon (1955) in Malaya, Lowe (1968) in Nigeria, and Medway (1972) and Poore

(1968) in Malaya. Janzen (1969, 1970) discusses the possible significance of this irregular flowering as an 'escape' from seed predation on a time basis.

Extended flowering occurred in many Wet forest species and was also observed in some Dry forest species. This flowering behaviour is perhaps significant in the light of recent suggestions by Janzen (1971 and personal communication) who has drawn attention to a rather distinct type of foraging behaviour possessed by large tropical bees (Euglossinae, Xylocopidae and Anthophoridae). He refers to this behaviour as 'traplining', in which foraging activity of the bee is such that it visits on a regular basis a widely spread series of plants to obtain a sufficient quantity of floral reward. Since many of the plants are of the same species, this movement allows for effective outcrossing of these species. The plants appear to be adapted to this foraging pattern since they accommodate the visitors by producing only a few flowers daily for extended time periods.

At the Wet forest site, Bunchosia swartziana, B. macrophylla, Cassia fruticosa, Stemmadenia donnell-smithii, and Swartzia simplex are all pollinated by representatives of the bee groups that Janzen discusses. At the Dry forest site, Cassia skinneri, Cochlospermum vitifolium, and Genipa caruto also attract 'traplining' bees.

In addition to the species visited by bees, the hummingbird-pollinated species *Erythrina* cochleata, Hamelia patens, Pentagonia donnell-smithii, and Warszewiczia coccinea and the moth-pollinated species Cestrum sp., Pithecolobium gigantifoliolum and the species of *Psychotria* also conform to this floral behaviour pattern. The respective pollinators of these tree species are probably all 'trapliners'. Baker (1973) presents evidence that some neotropical bats and the flowers they visit also fall into the 'trapline' syndrome.

Peak period in fruit maturation at the Dry forest site may be determined primarily by abiotic factors. However, two biotic factors may also affect the April peak (D. H. Janzen, personal communication). Firstly, succulent fruit will be more easily detected then because of the near leafless condition of the forest, and secondly they will be highly sought for the moisture which they contain. Therefore, fruiting in April takes place at the time when conditions for dispersal are optimal.

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SUMMARY

During 1969–70, 185 tree species at a Wet forest site and 113 species at a Dry forest site in Costa Rica were systematically observed for changes in leafing, flowering and fruiting.

(1) At the Wet forest site, the greatest amount of leaf fall in the overstorey and understorey trees occurred primarily during the first (more severe) dry season. At that time, 17% of the tree species from both storeys lost leaves.

(2) At the Dry forest site, the period of greatest leaf fall coincided with the long dry period; at that time 75% of the species lost leaves.

(3) Most Wet forest species flushed large quantities of new leaves during the first dry season. This was in contrast to the Dry forest site where most species flushed leaves at the onset of the first rainy season.

(4) Two apparent flowering peaks in the overstorey tree species and three apparent flowering peaks in the understorey tree species were recorded during the year at the Wet forest site. These major flowering periods in both layers occurred during wet as well as dry seasons, and two of the peak periods of the overstorey appeared to be out of phase with two of the understorey. The species at the Wet forest site were well represented by both 'seasonal' and 'extended' flowering species.

(5) At the Dry forest site, two peak periods of flowering activity were recognized. One extensive period occurred during the long dry season and a second peak period was recorded at the onset of the rainy season. Most species were of a 'seasonal' rather than 'extended' flowering nature.

(6) With regard to Wet forest fruiting, substantial numbers of species (at least 37) from both storeys were in mature fruit during each month, but a peak in fruiting occurred in both layers during the second dry season (August-October); the fruiting peaks of the two storeys were separated by one month. The disseminules of most Wet forest species were not adapted for wind dispersal.

(7) A peak period in the production of mature fruit occurred during the latter part of the long dry season at the Dry forest site. A significant proportion (31%) of the Dry forest species had disseminules adapted for wind dispersal.

(8) When phenological patterns of vicarious species of the two forests were compared, only flowering patterns showed similarity (11/27 species). Leafing and fruiting patterns of vicarious species tended to follow the general trends of the respective forest ecosystems.

(9) Periodicity patterns of most species in common between the two forest sites were similar.

(10) The phenological patterns recorded are discussed in relation to climatic 'triggers' (proximate factors) and plant-animal interactions (ultimate factors).

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APPENDIX

Lists of species recorded and their phenological behaviour are given below. Collection numbers are cited, in parentheses, for all plants not certainly determined to species level. The following initials are used for collectors; F, for G. W. Frankie; H, for G. S. Hartshorn; M, for H. E. Moore, Jr; O, for P. A. Opler. Abbreviations used in the lists are as follows:

NLD, no significant leaf fall observed;

CL, continuous production of a few new leaves;

DL, discontinuous production of new leaves;

US, unsynchronized flowering among individuals;

DA, difference in annual flowering intensity;

DP, difference in annual flowering periodicity.

List 1. Phenological records for overstorey tree species at the Wet forest site (for abbreviations see above)

Months of:

Speci	es	Leaf drop, leaflessness	Leaf flushing	Flowering	Mature fruit
1.	Alchornea costaricensis Pax & Hoffm	Dec.	Jan., Mar., Sep.	-	-
2.	Apeiba membranacea Spruce ex Benth.	Feb.	Mar.	May-June, AugSep.	MarApr.
3.	Astrocaryum standleyanum L. H. Bailey	(NLD)	(CL)	FebApr.	July-Sep.
4.	Bravaisia integerrima (Spreng.) Standl.	Nov.	Jan.	Jan., Oct., Nov. (US)	-
5.	Brosimum lactescens (Moore) Berg	(NLD)	Mar.–Apr. (DL)	Mar.	Мау
6.	Byrsonima aff. aerugo Sagot (H 1285)	Jan.–Feb.	FebApr.	Aug.	Oct.
7. 8.	Calophyllum brasiliense Camb. Carapa guianensis Aubl.	(NLD) (NLD)	Mar., May (DL) Feb., May (DL)	Sep. (DA) (Mar. 1972)	May
9.	Casearia arborea (Rich.) Urban	(NLD)	(CL)	MarApr., June-Aug.	May, Sep.
10. *11. 12. 13. 14. 15.	(Artin) Orbaila (L.) Jacq. Castilla elastica Cervantes Cecropia obtusifolia Bertol. Cedrela odorata L. Ceiba pentandra (L.) Gaertn. Cespedesia macrophylla Seem.	FebApr. (May-June) (NLD) JanFeb. Jan., Mar. (NLD)	AprMay (CL) (CL) Mar. Feb. Feb., Sep. (DL)	1/2 May-1/2 June May-June JanDec. May-June Jan. Mar. (Sen. 1973)	DecJan. June-July JanDec. Jan. Mar. May
16.	Cordia alliodora (B & P) Cham	Mar.–June	July–Aug.	JanFeb.	MarApr.
17.	Cordia dweri Nowicke	(NLD)	June (DL)	FebMar., SepOct. (DP)	AprAug. (JanFeb. 1971)
18. 19.	Cordia sp. III (H 1482) Dendropanax arboreus (L) Dec. & Planch	Jan. Feb.–Mar.	Feb. Feb.–Mar.	AprJuly June-July	July-Aug. 1/2 Aug1/2 Sep.
20.	Dialyanthera otoba	-	-	_	-
21.	Dipteryx panamensis (Pitt.) Record & Mell.	JanApr.	AprMay	May–July	NovFeb.
22.	Dussia cuscatlanica (Standl.) Standl. & Steverm.	Jan.	Feb.	Apr., Nov. (US)	SepOct.
23.	D. macroprophyllata (D. Sm.) Harms	Jan.	Feb.	Apr. (US)	May-June
24. 25.	Erythrina cochleata Standl. Eschweilera calyculata Pitt. vel sp. aff. (H 1097)	June-Sep. (NLD)	Sep. Mar. (DL)	June–Sep. (Aug., Oct. 1972) (Jan.–Feb. 1973)	Sep.–Oct. Apr.–June Aug.–Sep.
26. 27.	Euphorbiaceae (F 223) Genipa caruto H., B. & K.	(NLD) (NLD)	June (DL) Apr. (DL)	May, July-Aug. (DP) AprMay, OctNov.	Aug.
28.	Goethalsia meiantha	FebApr.	AprMay	July-Aug.	DecJan.
29. 30. 31.	Guarea guara (Jacq.) P. Wilson G. longipetiola C. DC. Guatteria aeruginosa Standi yal sp. aff. (H. 1008)	(NLD) (NLD) (NLD)	(DL) May, Nov. (DL) (CL)	Jan.–Feb. May, July Jan.–Dec.	Feb.–Mar. Mar. –May, Sep. Jan.–Dec.
32.	Hampea appendiculata	(NLD)	(CL)	July–Aug.	Jan.
33. 34.	Hasseltia floribunda H., B. & K. Heliocarpus appendiculatus	(NLD) (NLD)	(CL) (CL)	Apr.–Nov. Dec.–Jan.	DecFeb., July-Aug. JanMar.
35.	Hernandia didymantha D. Sm.	(NLD)	(CL)	FebMar. (DA)	May-June

* Lost leaves just prior to flowering; considered a continuous leafing species.

List 1 (contd)

		T C	Months	of:	
Speci 36.	es <i>H. stenura</i> Standl.	leaflessness (NLD)	Leaf flushing (CL)	Flowering MarApr., AugOct.	Mature fruit May
37. 38.	Hura crepitans L. Hyeronima oblonga (Tul.) Muell. Arg. var. benthamii (Tul.)	FebMar. (NLD)	Apr. (CL)	AprMay, OctNov. Jan., MarJune, Dec.	Feb. June–July
39. 40.	Muell, Arg. Ilex skutchii Edwin Inga coruscans H. & B.	(NLD)	Feb. (DL) MarApr., AugSep.	Feb. Feb., Sep. (DA)	AprMay, Sep.
41. 42. 43. 44	I. densiflora Benth. I. mimutula (Schery) Elias I. sapindoides Willd. I. thibadiana DC.	(NLD) (NLD) (NLD)	Feb., July, Sep. (DL) (CL) (DL)	Feb. (DA) Sep. (DA) Feb., AugSep.	Aug. Sep. SepOct.
45.	Inga sp. II (H 1326)	(NLD)	Feb. (DL)	Jan., July-Sep.	Dec.
46. 47.	Iriartea gigantea Wendl. Jacaratia costaricensis L. M. Johnston	(NLD) (NLD)	(CL) Mar. (DL)	MarApr. MarApr.	OctApr. AugOct.
48.	Lacmellea panamensis (Woodson) Marker	(NLD)	June (DL)	-	-
49.	Laetia procera (Poepp & Endl.) Endl	(NLD)	(CL)	May–July (US)	AugSep.
50. 51.	Lecythis costaricensis Pitt. Licania macrophylla Benth yel sp. aff. (H 1495)	Apr. (NLD)	May-June (DL)	May–July (Feb. 1974)	MarApr.
52.	Luehea seemannii	May	June	JanMar.	Apr.–May
53.	Miconia cf. calvescens DC.	(NLD)	(CL)	Mar., July-Oct.	AprMay, NovDec.
54.	Mimosaceae (H 1475)	-	Feb., June (DL)	July, Dec. (DA, DP) (Eab. 1972, 72)	AprJuly
55. 56.	Minquartia guianensis Aubl. Ochroma pyramidale (Cav. ex	(NLD) (NLD)	May (DL) (DL)	(Feb. 1972, 73) Jan. Dec.	Feb.–Mar. Mar.
57. 58.	Ocotea cooperi C. K. Allen O. mollifolia Mez & Pitt. Papilionaceae (F 313)	(NLD) (NLD)	(CL) Feb. (DL)	Feb. MarMay, Dec. Oct	AugSep. AugOct.
60.	Pentaclethra macroloba	(NLD)	Feb., Sep. (DL)	May-Aug.	July-Oct.
61.	Pithecolobium longifolium	-	(DL)	Feb.	-
62. 63. 64.	Pourouma aspera Trecul. P. umbellifera W. Burger Pouteria standleyana	(NLD) (NLD)	(CL) (CL) May (DL)	(Sep. 1975) 1/2 May-1/2 June July-Aug., Oct. Sep. (US, DA)	July-Sep. AprMay
65. 66.	(Pitt.) Baehni Protium sp. I (H 1476) Pterocarpus officinalis	(NLD) _	(DL) Feb. (DL)	Dec. 1/2 Feb1/2 Mar.	Jan.–Dec. July–Aug.
67. 68. 69.	Jacq. Rollinia microsepala Standl. Sacoglottis trichogyne Cuatr. Sapium pleiostachys	Nov.–Jan. (NLD) Mar.–May	Feb. Feb., June, Sep. (DL) (DL)	(SepOct. 1971) FebOct. July (DA)	July–Dec. May–July Sep.
70. 71. 72.	Schum, & Pitt. Sickingia maxonii Standl. Simarouba amara Aubl. Sloanea medusula	(NLD) (NLD) Feb.	Jan., Sep. (DL) (CL) Mar.	July–Sep. (DA) Feb. Feb., Aug.	Jan.–Dec. Apr. May, Aug.–Oct.
73.	Socratea durissima	(NLD)	(CL)	DecFeb., AprMay	JanDec.
74.	(Oerst.) Wendl. Sorocea sp. (H 1477)	(NLD)	June–July (DL)	May (DP)	1/2 July-Sep.
75.	Spondias mombin L.	Jan.–Feb.	Mar.–Apr.	(Feb. 1971) Feb1/2 May, July-Aug. (US)	Nov,-Dec. Sep,-Dec.
76. 77.	Sterculia recordiana Standi. Stryphnodendron excelsum	Dec. Jan.–Feb.	Jan.–Feb. Feb.–Mar.	Mar. (DA) Apr.–May (DA)	NovDec.
78.	Harms Tabebuia chrysantha	Apr.–May	-	-	-
79.	(Jacq.) Nicholson Tabernaemontana arborea	(NLD)	(CL)	MarApr.	JanMar.
80.	Rose Terminalia oblonga	(NLD)	May (DL)	Dec.–Jan. (DA)	Feb.–Mar.
81. 82.	(Ruiz & Pavon) Steud. Trema micrantha (L.) Blume Trichilla acutanthera	(NLD) (NLD)	(CL) (CL)	May-July Apr., AugSep.	Sep.
83.	C. DC. Trophis racemosa (L.) Urban	Feb.	Apr.	FebMar., AugOct.	1/2 DecJan.,
84.	Unonopsis pittieri Safford	(NLD)	(CL)	Jan., June-July, Sep.,	June-July Mar., AugOct.
85. 86.	Unonopsis sp. (H 1327) Veconcibea pleiostemona	(NLD) _	(CL) (DL)	Jan., May-June, Oct.	Jan., June–Oct.
87. 88. 89. 90. 91. 92.	(D. sm.) Fax & K. Hoffm. Virola koschnyi Warb. V. sebifera Aubl. Vietx cooperi Standl. Vochysia ferruginea Mart. V. hondurensis Sprague Xylopia sericophylla Standl. & L. Wms.	(NLD) (NLD) Mar.–May (NLD) (NLD) –	Jan., Aug. (DL) (CL) June-July Feb. (DL) FebMar. (DL) -	Feb., AugSep. (US) DecMar. 1/2 June-1/2 July May MarApr. (DA) -	JanFeb., May-Aug. June-Oct. Sep. AugSep. Aug. Dec. (FebMar. 1974)
93.	Zanthoxylum panamense P. Wilson	-	Apr. (DL)	May	Sep.

List 2. Phenological records for understorey tree species at the Wet forest site (for abbreviations see above)

Specie	25	Leaf drop, leaffessness	Leaf flushing	Flowering	Mature fruit
1.	Aegiphila falcata D. Sm.	*Variable	*Variable	AprMay, July-Aug.	AprMay,
2.	Anaxagorea costaricensis R E Fr	(NLD)	(CL)	MarNov.	AprJune, Aug.
3.	Andira inermis (Swartz) H., B. & K.	(NLD?)	Jan., June (DL)	(March 1972)	-
4. 5. 6. 7. 8.	Annonaceae II (F 397) Annonaceae III (F 414) Bactris sp. (M 10 123) Bombacaceae (F 124) Bunchosia macrophylla Rose ex D. Sm.	(NLD) (NLD) (NLD) Feb. (NLD)	Feb.–Mar. (DL) (CL) (CL) Feb. (DL)	Sep1/2 Oct. Feb. Aug. 1/2 Mar1/2 May July-Oct. (US)	Sep. OctNov. MarMay May SepFeb.
9.	B. swartziana Griseb.	(NLD)	(CL)	Feb., Apr., June, AugSen Nov. (DP)	AprMay, July-Oct.
10.	Capparis pittieri Standl.	(NLD)	(CL)	JanMar., May-June AugOct.	Feb., AprSep.
11. 12.	Cassia fruticosa Mill. Cassipourea elliptica (Swartz) Poir	Feb. (NLD)	Feb.–Mar. Feb.–Mar. (DL)	May-Oct. JanFeb., June-Aug	Oct.–Jan. July–Oct.
13.	Cestrum sp. (F 415)	(NLD)	(CL)	Mar., May, Sep. (US. DP)	Jan., July, Oct.
14. 15. 16. 17.	Chamaedorea pacaya Oerst. Chamaedorea sp. II† Colubrina spinosa D. Sm. Compsoneura sprucei (A. DC.) Warb.	(NLD) (NLD) (NLD) (NLD)	(CL) (CL) (CL) (CL)	(AprMay Apr. NovJan. FebMar. (♂ & ♀) AugNov. (♀) June-Sep. (♂)	OctDec. SepOct. FebApr. AprMay, OctNov.
1 8. 19.	Conostegia sp. (H 1478) Coussarea carolina	(NLD) (NLD)	(CL) Feb.–Mar. (DL)	MarApr. 1/2 June-1/2 July	June–July Sep.–Jan.
20.	C. taurina Standl. & L. Wms.	(NLD)	Feb. (DL)	1/2 Aug1/2 Sep.	NovDec.
21.	Croton schiedeanus Schlecht.	(NLD)	(CL)	July–Mar.	FebApr., Sen-Nov
22. 23.	Crysophila albida Bartlett Cymbopetalum costaricensis	(NLD) (NLD)	(CL) (CL)	June June, Sep.	Dec. Apr.
24.	Cyphomandra hartwegii (Miers) Dun.	(NLD)	(CL)	JanDec.	JanDec.
25.	Desmopsis maxonii Safford vel sp. aff. (H 1272)	-	-	-	Jan.
26. 27. 28.	Ficus tonduzii Standl. Flacourtiaceae? (F 409) Geonoma ?versiformis Wendl. ex Spruce (M 10 126)	(NLD) (NLD) (NLD)	(DL) Feb., May (DL) (CL)	Jan., Sep.–Oct. Sep.–Feb.	Aug. Feb., Nov. Feb., Aug., Oct.–Nov.
29. 30. 31. 32.	Grias fendleri Seem. Guarea rhopalocarpa Radlk. Guarea sp. (H 1451) Guatteria inuncta	(NLD) (NLD) (NLD) (NLD)	(DL) (CL) Feb. (DL) (CL)	– Feb., June, Sep. Mar. Sep.–Feb.	OctMar. SepNov. July-Oct.
33. 34. 35.	Hamelia patens Jacq. Heisteria concinna Standl. Henriettella tuberculosa D. Sm	(NLD) (NLD) (NLD)	(CL) Jan.–Feb. (DL) (CL)	Jan.–Dec. Nov.	Jan.–Dec. Sep.–Oct. (Feb. 1974)
36. 37.	Herrania purpurea (Pitt.) R. W. Schul. Hirtella lemsii	(NLD) _	(DL)	Jan.–Mar. Feb	AprJune (Feb. 1974) May
38.	L. Wms. & Prance H. racemosa Lam	(NLD)	Apr. Oct. (DI.)	Feb. Oct	Oct
39. 40.	Jacaratia dolichaula (J. D. Smith) Woodson Lonchocarpus oliganthus	JanFeb. (♀) NovMar. (♂) FebAnr.	Mar. (\mathcal{Q}) Apr. (\mathcal{J}) May-lupe	FebMar. (\mathfrak{g}) OctMar. (\mathfrak{g})	May–July Dec –Jan
41.	Hermann L. pentaphyllus (Poir.) DC	(NLD)	(DL)	(Nov.?) May	Aug -Sen
42.	Meliosma sp. (F 42)	(NLD)	(ČĽ)	May-Aug, (DP)	JanDec.
43.	Miconia sp. (F 57)	(NLD)	(CL)	July-Dec.	SepMar.
45.	Myrsinaceae (H 1449)	(NLD)	(CL)	1/2 June–Aug. Jan	AugDec.
46.	Myrtaceae I (H 1306)	(NLD)	(DL)	(June 1973)	Oct.
47. 48.	Myrtaceae II (H 1260) Nectandra aff. concinna Nees	(NLD)	(DL) (DL)	May-June, Aug. June-Oct.	Sep.–Oct., Dec. Sep.–Oct., Dec.
49.	Neea amplifolia D. Sm.	(NLD)	(DL)	Jan.–Feb., July–Sep. (US. DP)	FebApr., SepNov.
50.	Ocotea atirrensis Mez & D. Sm.	(NLD)	-	June	Nov.
51. 52. 53.	O. bernoulliana Mez O. cernua (Nees) Mez O. nicaraguensis Mez	(NLD) (NLD) (NLD)	(DL) Feb.–Mar. (DL) –	Aug. Mar.	Nov.–Mar. Sep.
54.	O. pedalifolia Mez	(NLD)	(DL)	Mar.	Dec.
55. 56. 57.	Ocotea sp. I (F 34) Ogcodeia naga (Pitt.) Mildbr. Pachira aquatica Aubl.	(NLD) .(NLD) _	(DL) Jan., Sep. (DL) Feb.–Mar. (DL)	Apr. Apr.–May (US, DA) Jan., Oct. (US, DA)	SepNov. May, SepOct. June-July

* Respective patterns depend on flowering-fruiting periodicities of individual plant. † Tree died after one year, no collection made. List 2 (contd)

List 2 (conta)							
		Months of:					
Specie	25	leaflessness	Leaf flushing	Flowering	Mature fruit		
58.	Parathesis chrysophylla	(NLD)	(CL)	(Mar. 1972) (DA) (Feb. 1974)	(May-June 1972)		
59.	Pentagonia donnell-smithii	(NLD)	(CL)	AprJuly (US)	FebMar., July,		
60.	Pithecolobium catenatum	(NLD)	(DL)	Jan., Mar., June	May, Aug., Oct.		
61.	P. gigantifoliolum (Schery) I. León	(NLD)	(DL)	1/2 June-1/2 July	Nov.		
62.	Posoqueria latifolia (Budge) Roem & Schult	(NLD)	(DL)	Mar.–Apr., June (DA)	OctJan.		
63. 64.	Posoqueria sp. (H 1479) Pouteria lucentifolia (StandL) Baehni	(NLD) (NLD)	Feb.–Mar. (DL) (CL)	Mar. (DA) May-June	Nov., Dec. Jan.–Dec.		
65. 66. 67.	P. neglecta Cronquist Pouteria sp. I (H 1137) Prestoea decurrens	(NLD) (NLD) (NLD)	Apr. (DL) (DL) (CL)	(DA) (May 1972) (DA) Jan.–Dec.	June, Sep.–Jan. Nov.–Mar. Jan.–Dec.		
68. 69.	(Wendl. ex Burret) H. E. Mo Protium glabrum (Rose) Engl. Protium sp. (F 56)	ore (NLD) (NLD)	Feb., May (DL) Feb., Sep. (DL)	June, SepOct. JanFeb., May-Sep.	Jan.–Dec. Jan.–Dec.		
70. 71.	Psychotria sp. II (H 1368) Quararibea sp. (F 222)	(NLD)	(DL)	Mar. Mar.	OctJan.		
72.	Randia armata (Swartz) DC.	Mar.	Mar.	Aug. (DA) (Feb. 1974)	Jan.		
73. 74.	R. grandifolia (D. Sm.) Standl. Rauvolfia tetraphylla L.	(NLD) (NLD)	Apr. (DL) (DL)	Apr. Jan., 1/2 June–July (DA DP)	July, Sep.–Oct.		
75.	<i>Rheedia edulis</i> Triana & Planch.	(NLD)	JanFeb., SepOct. (DL)	Jan., 1/2 Sep1/2 Oct.	-		
76.	Rinorea pubipes Blake	(NLD)	Mar. (DL)	Dec.–Jan.	Feb.		
77.	Rubiaceae (H 1480)	(NLD)	(CL)	Aug.	JanFeb.		
78.	Ryania speciosa var.	(NLD)	(DL)	FebMar., Sep.	Mar.–Apr., Oct.		
79.	Sapranthus campechianus (H., B. & K.) Standl	Dec.	Dec. (DL)	-	Sep.		
80.	Siparuna nicaraguensis Hemsl	. (NLD)	(CL)	Jan.–Dec.	Jan.–Dec.		
81.	Siparuna sp. I. (H 1481)	(NLD)	(CL)	Feb., Apr.	July-Oct.		
82.	Siparuna sp. II (F 341)	(NLD)	(CL)	Aug.–Mar.			
83.	Sloanea faginea Standl.	(NLD)	(DL)	- N/ (0)	SepNov.		
84.	Sorocea pubivena Hemsl.	(NLD)	Feb. (DL)	June, Nov. (\mathfrak{P}) Nov. (\mathfrak{Z}) (DA, DP)	AugSep., DecJan.		
85.	Stemmadenia donnell-smithii (Rose) Woodson	(NLD)	(CL)	JanDec.	JanDec.		
86.	Swartzia simplex (Swartz) Spreng.	(NLD)	(CL)	Jan., May-Sep. (US)	JanMar., June-Nov.		
87. 88.	Symphonia globulifera L. f. Synechanthus warszewiczianus Wendl,	(NLD) s (NLD)	(DL)	JanDec. June	June-July, NovDec. OctJan.		
89.	Tovomotopsis multiflora Standl.	Mar.	Mar. (DL)	JanFeb., AugSep. (US)	FebApr.		
90. 91.	Vismia latifolia Choisy. Warszewiczia coccinea Wahl Klotzsch	(NLD) (NLD)	(CL) (CL)	Jan.–Feb., July–Aug. Jan.–Dec.	Mar., Nov. Jan.–Dec.		
92.	Welfia georgii Wendl.	(NLD)	(CL)	JanDec.	JanDec.		

List 3. Phenological records for tree species at the Dry forest site (for abbreviations see above List 1) Months of

		Months of:				
Species		Leaf drop, leaflessness	Leaf flushing	Flowering	Mature fruit	
1. 2.	Achras zapota L. Albizia caribaea	May-June	July	June Mar.	Oct.–Nov. Mar.	
3.	(Urban) Britt. & Rose A, longepedata (Pitt.) Britt. & Rose	Jan.	Jan., Apr., Sep.	Jan.	Apr.	
4.	Alvaradoa amorphoides Liebm.	Mar.–Apr.	May	1/2 Oct1/2 Nov.	Mar.–Apr.	
5.	Anacardium excelsum (Bert, & Balb.) Skeels	Dec.	Jan., July	Feb1/2 Apr.	Apr.–May	
6.	Andira inermis (Swartz) H B & K	Nov.	Nov.	Feb. (DA)	May-June	
7.	Annona purpurea Moc. & Sessé	Jan.–May	June	Apr.	July	
8.	A. reticulata L.	DecFeb.	AprJune	AprOct.	DecFeb.	
9.	Apeiba tibourbou Aubl.	Feb.–Mar.	May-June	May–Nov.	AprMay	
10.	Astronium graveolens Jacq.	Dec., July	Dec., July	(Jan. 1971) (DA)	(Dry season)	
11.	Bombacopsis quinata (Jacq.) Dugand	NovApr.	June	Feb.–Mar.	Apr.	
12.	Bourreria guirosii Standl.	Feb1/2 Apr.	May/June	AugApr.	Jan.–Dec.	
13.	Brosimum costaricanum Liebm.	(NLD)	1/2 May-1/2 June (DL)	(Dry season)	May–June (Feb. 1974)	
14.	Bursera simaruha (L.) Sarg.	NovMar.	Mav-June	Apr1/2 May	Apr.	
15.	B. tomentosa (Jacq.) Triana & Planch	OctApr.	May-June	May–Aug.	AugOct.	
16.	Byrsonima crassifolia (L.) DC.	(NLD)	Feb.–Mar. (DL)	Feb1/2 May	May–July	

Months of:

List 3 (contd)

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			Month	s of:	
6		Leaf drop,	Loof Auching	Flowering	Matring fruit
Speci	es	leanessness	Lear nusning	Flowering	Mature truit
17.	Caesalpinia coriari	Mar.	Apr.	Sep. (DP)	DecJan.
	(Jacq.) Willd.				
18.	C, eriostachys Benth.	Jan.–Feb.	1/2 FebMar., June	Jan.–1/2 Mar.	Apr.
19.	Calycophyllum candidissimum	Jan.–Mar.	May–June	1/2 Nov.–Jan.	Mar.–Apr.
	(Vahl) DC.			-	<u> </u>
20.	Casearia aculeata Jacq.	Jan.–Mar.	Apr.–May	June	Sep.
21.	C. arborea (Rich.) Urban	FebApr.	Мау	Oct.	Apr.–May
22.	Cassia skinneri Benth.	Dec.–Apr.	June	SepNov.	DecJan.
23.	C. grandis L. I.		Mar., June-July	1/2 FebMar.	Dry season
· 24.	Cecropia peitata L.		June (CL)	AprAug.	May-Sep.
23.	Ceareia odorata L.	JanApr.	Variable	June Jon (DA)	reo.
20.	(I) Gaertn	V al lable	v al lable	Jan. (DA)	Apr.
27	Chlorophora tinctoria	Ian – Mar	Apr – June	June-Sen	June-Sen
27.	(L.) Gaud	built inful?	Tipi: Vane	June Bep.	vane bep.
28.	Chomelia sninosa Jaca.	JanFeb.	AprJune	July-Aug.	SepOct., Dec.
29.	Clusia rosea Jaca.	(NLD)	_	June-July	Jan-Apr.
30.	Coccoloba padiformis Meisn.	1/2 Jan1/2 Feb.	1/2 FebApr.	Feb.	Apr.
31.	Cochlospermum vitifolium	DecMar.	May	Jan.–Feb.	Mar.–Apr.
	(Willd.) Spreng.				
32.	Cordia alliodora	Feb.–Apr.	May	1/2 Jan.–Feb.	Apr.
	(R. & P.) Cham.			_	
33.	C. panamensis Riley	Jan.–Mar.	Jan., May	June	AugSep.
34.	Crescentia alata H., B. & K.	AprMay	June	AprNov. (US)	Mar.–Apr.
35.	Curatella americana L.	Jan.–Feb.	FebMar., July	JanFeb.	Apr.
30.	Daibergia refusa Hemsi.	Jan.–Mar.	Apr.	1/2 Mar. $-1/2$ Apr.	Dry season
27	Diagnuman nigan anuangia	Eab Mas	A	(DA) May	1/2 Nov Feb
57.	Stand	rebIviai.	Apr.	Iviay	1/2 11041100.
38	Enterolobium cyclocarnum	Ian _Feb	Mar	Anr	Ant
50.	(Jaca) Griseb	Jan1 CD.	Mai.	Apr.	Apr.
39.	Erythroxylon lucidum H. B & K	Anr – May	1/2 May-June	First 1/2 June	_
40.	Ervthroxylon sp. (F 379)	JanApr.	May	End Mar.	Dry season
41.	Eugenia salamensis D. Sm.	FebApr.	1/2 May-1/2 June	First 1/2 June	Sep.
	var. hiraeifolia (Standl.) McV.				•
42.	Exostema ?mexicanum Gray	Mar.–Apr.	May	July	FebApr.
	(F 323)	-	-	-	-
43.	Ficus sp. (0 2112)	-	-	-	Oct.
44.	Genipa caruto H., B. & K.	Jan.–Apr.	May-June	June-1/2 July (DP)	Apr.–May
45.	Gliricidia sepium	Nov.–Mar.	May–July	Jan.–Feb.	Apr.
	(Jacq.) Steud.				D D I
46.	Godmania aesculifolia	JanFeb.	Apr.	Apr.–May	DecFeb.
47	(H., B. & K.) Standl.		Inter (DI)	Turne	Ann More
47.	Guarea luxii C. DC.	(NLD)	June (DL)	June	AprMay
40.	Guattarda Imacrosporma	JanMar	Apr.	June	FebMar.
ч <i>у</i> .	D. Sm. (F 249)	JanMar.	1/2 AprJune	June	July
50.	Hemiangium excelsum	Mar1/2 Apr.	1/2 Apr -1/2 May	Mar – Anr	FebMar.
	(H., B. & K.) A. C. Sm.		1/2p.: 1/2uj	in and input	
51.	Hura crepitans L.	OctNov.	Apr.	AprJuly	Aug., Nov.
	-	Jan.–Mar.	•	1/2 SepNov.	
52.	Hymenaea courbaril L.	Jan., July	Jan.	1/2 Mar1/2 Apr.	Dec.–Jan.
53.	Ixora floribunda	(NLD)	(DL)	Dec.–Jan.	-
	(A. Rich.) Griseb.				
54.	Karwinskia calderoni	MarJune	July	July	Wet season
	Standi.	D. M.		26	T
55.	Liegnia arbarea Seem	DecMar.	1/2 AprMay	Mar., Apr.	June-July
57	Lonchocarpus costanicensis	Lop Mor	DecJan.	1/2 Mos $1/2$ App	May Jupe
57.	(D Sm) Pitt	JanMai.	AprMay	1/2 Mar1/2 Apr.	May-June
58.	L. eriocarinalis Micheli	JanMay	June	Apr. (DA)	1/2 NovDec.
59.	L. nitidus (Vog.) Benth.	FebApr.	May-June	Oct1/2 Nov.	Apr.
60.	L. orotinus	FebMar.	AprMay	June	-
	Pitt. vel sp. aff. (F 385)				
61.	L. phaseolifolius Benth.	Jan.–1/2 Apr.	1/2 Apr.–May	1/2 AugSep.	1/2 NovDec.
62.	Luehea candida (DC.) Mart.	Jan.–Apr.	May-June	June	Feb.–Mar.
63.	L. speciosa Willd.	Mar.–Apr.	1/2 Apr.–May	DecJan.	Mar.–May
64.	Lysiloma auritum (Schl.) Benth.			Feb1/2 Mar.	Dry season
65.	L. Seemannii Dritt & Dooo	Jan.–May	1/2 June–July	July	JanFeb.
66	Machaenium biouulatum	Mar	Aug. Mars	A	Dee Jen
00.	Micheli	Mai.	AprMay	Aug.	DecJan.
67	Malpighia tomentosa	_	May June	July Oct	Feb ?
•	Sessé & Moc.		May-June	July, Oct.	100
68.	Mastichodendron capiri	Dec	Ian	Feb _Mar	Anr – Mav
	(A. DC.) Cron, var. tempisaue				
	(Pitt.) Cron, vel sp. aff. (F 116)				
69.	Miconia argentea (Swartz) DC.	Mar.–June	July	1/2 DecJan.	AprMay
70.	Muntingia calabura (Swartz) DC.	(NLD)	(CĽ)	JanDec.	Jan.–Dec.
71.	Myrospermum frutescens Jacq.	DecMar.	May	1/2 Feb1/2 Mar.	Apr.
-				(DA)	
72.	Ochroma pyramidale	Мау	1/2 May–June	DecJan.	Mar.
	(Cav. ex Lam.) Urban		L. P.L (DV)	T. T.I	A
13.	(Meisn) Mez	(INLD)	JanFeb. (DL)	Jan,-Feb.	Арг.
74	Olacaceae (F 381)	Ant			_
75	Papilionaceae (F 416)	Ian	1/2 Jan _Anr June	(Dry season) 1/2 Jan -1/2 Feb	-
76	Piscidia carthagenonsis Taca	Mar – Anr	May	1/2 Jan1/2 100.	May
				(DA)	
				· · · · /	

* Each individual produced a few new leaves per month with the exception of June.

List 3 (contd)

LISt	5 (comu)		Month	us of	
Speci	es	Leaf drop, leafiessness	Leaf flushing	Flowering	Mature fruit
77. 78.	Pisonia macranthocarpa D. Sm. Pithecolobium dulce	(NLD) _	Apr. (DL) May-June	Aug., Sep. First 1/2 Apr.	_ Apr.–May
79.	(Roxb.) Benth. P. longifolium (Humb. & Bonpl.) Standl.	(NLD)	Feb. (DL)	(Dec., Jan. 1971) First 1/2 Sep., 1/2 Oct1/2 Nov. (end Dec.) (DA, DP)	June
80. 81.	P. saman (Jacq.) Benth. Platymiscium pleiostachyum D. Sm.	Mar. Dec.	Mar. Jan.–Feb.	Apr. $1/2$ Jan. $-1/2$ Feb. (DA)	Mar. Apr.
82. 83.	Plumeria rubra L, Pouteria sp. (F 383)	OctMar. (NLD)	Apr. June (DL)	MarJune June	Dec.–Jan. July
84.	Pseudobombax septinatum (Jaco.) Dugand	DecMay	June	Jan1/2 Mar.	AprMay
85.	Psidium sartorianum (Berg.) Ndzu.	Jan.–Apr.	May–June	First 1/2 July	DecJan.
86.	Pterocarpus rohrii Vahl	Jan.–Mar.	Apr.	1/2 Feb1/2 Mar. (DA)	Apr.–May
87.	Rehdera trinervis (Blake) Moldenke	Jan.–Apr.	Мау	June	DecJan.
88. 89.	Rheedia edulis Triana & Planch. Sapium thelocarpum Schm. & Pitt yel sp. aff. (F 382)	(NLD) Dec.–Apr.	Jan. (DL) June	Jan. June	Feb. Wet season
90. 91. 92.	Sapranthus palanga Fries Schoepfia schreberi Gmel. Sciadodendron excelsum Griseb	Feb.–Mar. (NLD) Jan –Mar	May–June Apr. (DL) May	1/2 JanMar. Feb. 1/2 Apr1/2 May	July Apr. June–July
93. 94.	Simarouba glauca DC. Sloanea terniflora (Moc. & Sessé) Standl.	(NLD) (NLD)	Jan. (DL) Jan.–Feb. (DL)	Jan.–Feb. Jan.	Mar. Apr.–May
95. 96.	Spondias mombin L. S. nigrescens Pitt.	Jan.–Mar.	Apr.–May	AprMay	Sep. Sep.
97. 98.	S. purpurea L. Sterculia apetala (Jacq.) Karst,	Jan.–Mar. –	May Mar., June	JanFeb. Feb., Mar., Sep. (US)	Apr. DecMar.
99. 100.	? Stillingia sp. (F 376) Styrax argenteus Presl. var. argenteus	(NLD)	Jan. (DL)	Apr. Nov.	Dry season –
101.	Swartzia myrtifolia J. E. Smith	MarApr.	Мау	Nov.	FebApr.
102. 103. 104.	Sweetia panamensis Benth. Swietenia humilis Zucc. Tabebuia neochrysantha	Jan.–May (NLD) Dec.–Apr.	July Jan., Mar., June (DL) May	Aug.–Sep. Feb.–Mar., July End Mar. (DA)	Dec.–Jan. Jan. Apr.
105. 106. 107. 108.	A. Gentry T. palmeri Rose T. rosea (Bertol.) DC. Thevetia ovata (Cav.) A. DC. Thouindium decondrum	DecApr. JanMay JanMar. (NLD)	May June May Jan – Feb. (DL)	End Jan. (DA, DP) FebMar. AprSep. 1/2 Jan -Feb.	Mar. Apr.–May May–Nov. Mar.
109.	(Humb. & Bonpl.) Radlk. Trichilia cuneata	Mar.	Apr.	Mar1/2 Apr.	June-July
1 10. 111.	Radkl. vel sp. aff. (F 161) T. tomentosa H., B. & K. Ximenia americana	Jan.–Apr. Feb.–Mar.	May–July Mar.	June-July Mar1/2 Apr.	Feb. Apr.
112. 113,	L. var. americana Zanthoxylum sp. (F 417) Tree No. R1-133.5 (F 413)	Jan.–Mar. (NLD)	May	1/2 Apr1/2 May	AugSep.