Phenology and Other Characteristics of Tropical Semi-Deciduous Forest in North-Western Costa Rica

Rexford Daubenmire

Journal of Ecology, Vol. 60, No. 1 (Mar., 1972), 147-170.

PHENOLOGY AND OTHER CHARACTERISTICS OF TROPICAL SEMI-DECIDUOUS FOREST IN NORTH-WESTERN COSTA RICA

BY REXFORD DAUBENMIRE

Washington State University, Pullman, Washington, U.S.A.

During the rainy season the semi-deciduous forest in tropical north-western Costa Rica bears a close rememblance to deciduous forests of temperate eastern U.S.A. and central Europe in their summer aspect. This physiognomic resemblance is ecologically striking since the former temperature varies but little through the year with rainfall differing markedly, whereas in the latter precipitation is abundant at all seasons but temperatures are strongly contrasted between summer and winter. During a year's residence in the Costa Rican forest, records were made of tree growth, flowering, and fruiting with the objective of characterizing such features of the vegetation more closely than has yet been done, and where feasible drawing comparisons with the temperate zone forest.

Table 1. *Climatic data for Cañas (La Pacifica), as recorded at the official weather station located* 1·8 *km from the study site (Serv. Met. Nac.,* 1963)

	Median rainfall (mm)	No. rainy days	Temperature (°C)			Extreme temp. (°C)		Rel. Hum. (%)			Piche evap. (ml/day)	Mean h sunshine
			Mean max.	Mean	Mean min.	Max.	Min.	Mean max.	Mean	Mean min.		
Jan.	0	1	31·5	27·4	23·2	35·0	22·0	88	71	53	11·8	8:00
Feb.	0	3	32·6	27·6	22·5	35·5	20·5	84	66	45	12·2	8:54
Mar.	0	2	33·3	29·0	24·6	35·5	23·0	80	62	46	15·6	9:42
Apr.	7·6	9	32·7	28·3	23·6	35·0	20·5	87	71	51	9·5	7:18
May	165·2	5	34·1	29·2	24·4	35·5	22·5	90	73	52	10·9	7:57
June	259·1	15	32·5	27·9	23·3	36·0	21·0	97	79	55	6·3	5:36
July	149·1	9	32·5	27·5	22·8	34·5	21·5	96	77	53	–	5:00
Aug.	186·0	8	33·5	28·4	23·3	35·0	20·5	92	74	51	–	6:48
Sep.	350·0	18	33·8	28·0	22·1	36·5	20·5	89	82	54	7·3	5:06
Oct.	358·4	20	32·3	27·0	21·8	34·5	20·0	98	80	52	6·7	6:12
Nov.	63·4	13	30·0	26·2	22·5	33·0	20·0	96	79	59	7·1	5:06
Dec.	0	3	30·4	27·0	23·5	34·0	20·0	86	73	56	10·0	–
Year	1538·8	106	32·4	27·8	23·1	–	–	90	74	52	–	–

All columns are for 1963 except for temperature extremes and median rainfall, which are based on all records until and including 1963. The mean rainfall for the same period of years (1951–1963) is 1926 mm. The evaporimeter was housed in a louvered screen.

The study was made in the vicinity of Cañas, Gaunacaste Province, Costa Rica. Climatic characteristics of the area are indicated in Table 1.

The initial plan was to study three groups of trees in contrasted habitats. One group of fourteen species represented the upland forest which once occupied all zonal soils of the region. A second group of thirteen trees represented the arboreal element of savanna which has been derived from the upland forest. Fourteen additional species of trees represented the strips of mainly evergreen riparian forest. It was eventually learned that the savanna trees were but accidental survivors of the forest flora rather than an ecologically distinct group, so that data for these two physiognomic types were pooled to make a more substantial group representating upland forest.

Records presented more fully in another connection (Daubenmire 1971) show that during the dry season the soil profile in upland forest dried to the wilting point to a depth of about 30 cm in 1970, with this condition lasting from mid-February to mid-May. The soil of the savanna was similar except for the presence of frequent small outcroppings of the pumice that underlies all soils in the area. Trees growing along the river had their roots unquestionably in contact with abundant soil moisture of the narrow sandy floodplain throughout the year, and several times in the rainy season water rose briefly to surround the bases of their trunks.

For the most part each species of tree was represented by a single individual, since the objective was to characterize the tree stratum as a whole rather than the average behaviour of individual species. However, three species in the upland forest and two in the savanna were also represented in the riparian group, so that in these species there was opportunity to compare responses in wet and dry environments. In addition to the forty-one indigenous trees, one individual in a plantation of *Tectona grandis* was studied. Although the seed source of this plant was unknown, most ecotypes of the species occur in somewhat comparable seasonal climates of the Indo-Malaysian region. Some of the species studied here in north-western Costa Rica have received attention in the more uniformly moist climate of the Caribbean coast of Costa Rica, or elsewhere, so that regional comparisons are possible.

The study extended from 23 July 1969 to the same day of the following year, a period starting one-third into the rainy season of one year and continuing through the dry season to the same point in the next rainy season.

METHODS

Radial changes in tree trunks were measured with a dendrometer like that described originally by Daubenmire (1945), except that the base plate was made of cast and machined aluminium (Plate 1) rather than hardwood faced with stainless steel, and the wood screws fixed in the trees were of stainless steel rather than of brass. This instrument records radial changes in 0·001 in. (0·025 mm). Two settings were installed on each tree, on different radii. Any roughness or loose scales at the point where the spindle of the dial gauge struck the tree were sliced off with a sharp knife to leave a smooth surface of phellem at this point. Readings were made as early in the morning as feasible to minimize the effect of the daily reduction of turgor on apparent seasonal trends in radial change.

The trees were measured weekly with but two exceptions. Records at the beginning and end of the last month, the longest break, are connected by broken lines in the graphs to indicate that possible variations in growth rate during this month are unknown. Also, records of two species were started late, and the arbitrary starting points for graphing these represent estimates of the amount of unrecorded growth. Since both types of breaks in the records involve the rainy season when growth was relatively rapid and regular, the loss of detail at this season is probably of small consequence.

Several species showed rather violent changes in radius within a 7-day period. Since each measurement was checked three times, and two instruments were available on each tree for comparison, there seems to be little chance for these fluctuations to represent

Dendrometer made by attaching a machinist's dial gauge to an aluminium platform which is placed against permanently set screws. A rim around the sides and top of the platform allows exact replacement of the instrument if the rim is fitted against the top two screws in the same manner at sequential readings. The screws penetrate the tree for more than half their length. (Photograph by R. Daubenmire.)

error in measurement. A swelling of the bark when wetted directly by rain might be suspected of causing sudden radial increase should a heavy rain follow a dry interval. Since lengthenings of this terminal segment of a radius are of no ecologic consequence, yet would appear as growth, they are considered error. To test the degree of error of this type, the bark of nine species that showed sharp fluctuations in radius was wetted immediately after the usual morning readings during dry weather; then the instruments were read again late in the afternoon, with the bark kept wet during the intervening hours.

As pointed out earlier, there were two instrument settings for each tree. Only one member of the pair was wetted. A pad of many thicknesses of water-soaked cotton cloth was placed against the bark and a generous patch of waterproof plastic sheeting was then stretched over the pad and held in place with pins around the margin. At mid-day the trees were revisited and water from a wash bottle added to ensure continued saturation of the pad. Just before dusk the pads were removed and new readings of both the wetted and the dry instruments were made for comparison with morning values.

Table 2. *Influence of wetting the outer bark on the length of trunk radii during approximately an 8-hour period*

Tree species	Net change in 0·001 in. (0·025 mm) June 9	June 16
Swietenia macrophylla	+16	+17
Tabebuia neochrysantha (riparian)	+5	+3
Platymiscium dimorphandrum	+3	+3
Sapranthus pallanga	+1	+4
Luehea candida	+2	+1
Manilkara spectabilis	−2	+3
Tabebuia neochrysantha (upland)	+1	−2
Guazuma tomentosa	+4	−5
Days since last rainfall	1	5

The radius of the dry instrument would be expected to shorten during the day owing to the usual development of water deficit in the living tissues. The same decrease in the other radius would be expected to be offset by a swelling of the outer layer of phellem that had been kept hydrated by surface applications of water. The differences in changes recorded on the two radii during the approximately 8-h period should then reflect the amount of swelling attributable to wetting of the outer bark.

The differences observed (Table 2) were small except in *Swietenia* (for species and name authorities see Table 3). The fact that radii appeared to shrink twice instead of swell after wetting suggests that none of the results except those for *Swietenia* indicated changes in bark thickness. Usually any two instruments on a tree vary somewhat in the amount of radial changes they indicate, and the radial changes noted in these tests are, except for *Swietenia*, within the range of such random variations of behaviour. Inconsistency in the results of the test repeated on the same trees on different days, except again for the one species, strengthens this interpretation. Also, it is to be noted that seldom would a rain storm be as effective in keeping the bark so wet for so long a period as the 8-h test.

In summary of the above, it appears that except for all but one species swelling and shrinking of the outer bark that might result from surface wetting and drying is not a significant component of the violent radial changes that were sometimes recorded. However, in *Swietenia macrophylla* as much as 0·432 mm of radial increase could be attributed to direct wetting of the bark, providing the rain storm was of sufficient

Table 3. *Maximum radial shrinkage in* 0·001 *inch* (0·025 *mm*) *observed during the dry season, based on the highest previous reading of the preceding wet season, and net radial increment during the year*

	Shrinkage	Increment	Fig.
UPLAND			
Savanna			
Tabebuia neochrysantha A. Gentry	87·5	292	13c
Guazuma tomentosa HBK.	50·0	125	3b
Cordia alliodora (R. & P.) Cham.	38·0	302	4a
Chomelia spinosa Vacq.	36·0	22	3a
Dalbergia hypoleuca Pittier	23·5	48	5a
Godmania aesculifolia (HBK.) Standl.	21·5	78	4c
Cordia stellifera I. M. Johnst.	19·5	424	4b
Lonchocarpus minimiflorus D. Sm.	15·5	241	5b
Enterolobium cyclocarpum (Jacq.) Gris.	14·5	102	8c
Machaerium biovulatum Micheli	12·0	182	8a
Chlorophora tinctoria (L.) Gaud.	10·5	94	5c
Pterocarpus hayesii Hemsl.	3·5	182	14a
Piscidia carthagenensis Jacq.	1·5	56	3c
Forest			
Tabebuia neochrysantha A. Gentry	97·0	132	13a
Manilkara spectabilis (Pitt.) Standl.	86·5	174	1b
Bursera simaruba (L.) Sarg.	80·0	60	1a
Tectona grandis L.	76·5	454+	14b
Sapranthus palanga Fries	71·5	34	9a
Platymiscium dimorphandrum D. Sm.	71·0	156	9c
Spondias purpurea L.	62·5	316	10a
Luehea candida (DC.) Mart.	52·0	90	1c
Cochlospermum vitifolium (Willd.) Spreng.	33·5	234	6b
Bombacopsis quinata (Jacq.) Dugand	29·5	257	11c
Lysiloma sp. (Daubenmire #47)	21·5	176	9b
Guettarda macrosperma Donn. Sm.	17·0	21	6a
Trichilia colimana C. DC.	10·5	222	6c
Sterculia apetala (Jacq.) Karst.	8·5	459	11b
RIPARIAN			
Facultative phreatophytes			
Tabebuia neochrysantha A. Gentry	75·0	149	13b
Swietenia macrophylla G. King	73·5	54	12a
Spondias purpurea L.	59·0	224	10b
Calycophyllum candidissimum (Vahl) DC.	25·5	14	2a
Spondias mombin L.	25·0	−25	10c
Sterculia apetala (Jacq.) Karst	4·5	210	11a
Enterolobium cyclocarpum (Jacq.) Gris.	3·0	205	8b
Obligative phreatophytes			
Hymenaea courbaril L.	8·0	123	7a
Anacardium excelsum (Bert. & Balb.) Skeels	8·0	87	7b
Ceiba pentandra (L.) Gaertn.	6·6	83+	2c
Licania arborea Seem.	2·0	252	7c
Coccoloba caracasana Meisn.	1·0	268	12b
Sloanea terniflora (Moc. & Sessé) Standl.	0·5	138	12c
Inga spuria Humb. & Bonpl. ex Willd.	0·0	704	2b

magnitude and from an appropriate direction to keep the bark wet for at least 8 h. Since the instruments were not on the same radius, only one was likely to be wetted by even this unusual circumstance. Therefore approximately half of the average value of the two instruments (i.e. 0·216 mm) would represent error. The magnitude of this possible source of error is indicated on the graph (Fig. 12a) representing radial changes of *S. macrophylla*.

In the first use of this type of dendrometer a small metal plate was glued to the bark surface to protect the point of impingement of the dial gauge spindle. Had this been done for *Swietenia* the possible wetting-and-drying error would have been minimized if not avoided.

In this study the phenologic aspects of radial changes have been considered of more importance than the amount of growth. Therefore, to make comparisons easier the actual measurements have been converted to percentage values based on the net difference between measurements at the start and end of the year's study. The net radial change observed during the year, as well as the maximum shrinkage observed during that year, are indicated in Table 3.

Each week the tree canopies were scanned with field glasses so that the state of development of leaves, flowers and fruits could be recorded. Conditions noted in the field and indicated on the graphs were as follows.

(a) Foliage: young leaves expanding; mature, healthy leaves present; some or all of leaves senescing, i.e. discolouring or simply dropping while still green, owing to internal changes rather than insect damage or disease; leafless.

(b) Reproductive activity: pollinating; immature fruits present after pollination ended but before dissemination commenced; dissemination in progress.

The phenologic record refers to only the individual studied, rather than to the species as a population, for there is often considerable variation among individuals. As in temperate and cold climates, trees in this region do not necessarily flower each year, and it is possible that their growth and internal water balance may differ somewhat when the plant flowers and fruits abundantly from when it remains vegetative. Where the 'pollinating' symbol ends without being followed by 'immature fruit' or 'disseminating', no fruit was set. 'Immature fruit' not followed by 'disseminating' resulted from monkeys eating all the fruit before it ripened (as in *Spondias mombin*), or fruit dropping prematurely for any reason. In the riparian forest *Enterolobium* flowered so feebly that this event passed unnoticed, and the first recognition of reproductive activity was made only after the fruits started to grow.

An effort was made to collect voucher specimens for all individuals studied, but where the canopy was far above the ground, or the individual studied did not flower, this was not possible, and identification rests on apparent similarity to other individuals for which taxonomically critical material was collected. Some use could be made of fallen fruits, leaves or foliage sprays broken off by monkeys. The vouchers have been filed in the herbaria of Washington State University in Pullman, the Field Museum of Natural History in Chicago, and the University of Costa Rica in San José.

RESULTS AND DISCUSSION

The basic data for radial changes, flowering and fruiting, leaf production and senescence are shown graphically in Figs. 1–14. Table 4 presents the summarized behaviour of the trees as ecologically homogeneous groups. If the phenology of these trees is viewed

Table 4. *Percentage of tree species exhibiting a particular type of behaviour on different observation dates (the first three columns are based on twenty-five species, the next two on twenty-four and twenty-two, respectively, and the last two only seven species; the average dry season falls between the two broken lines)*

		Upland forest and savanna					Riparian		Normal rainfall (mm)
		Flushing	Senescing	Leafless	Pollinating	Disseminating	Flushing	Senescing	
July	23	16	8		4	5			
	25	16	8		4	5			149
	29	16				5			–
Aug.	6	16			4	5			
	12	16			8	5			186
	19	20			8	5			
	26	36				5			–
Sep.	2	40							
	9	40					14		
	16	36					14		350
	23	32					14		
	30	36					14		–
Oct.	14	40	4				14	14	
	21	36					14	14	358
	28	36	12			5	14	29	–
Nov.	4	28	8		4	5	14	14	
	11	20	12			5	14	43	63
	18	16	24		4	5		14	
	25	24	24		4	9		43	–
Dec.	2	24	44		8	9	14	43	
	9	16	36		8	9		43	
	16	8	44		4	9		57	0
	23	4	44		4	14	14	43	
	30		52		8	14	14	43	–
Jan.	6		52	4	8	9	14	43	
	13		64	4	17	14	29	43	0
	20	8	76	8	13	18	29	43	
	27	4	60	12	17	23	57	43	–
Feb.	3	12	64	16	29	18	57	2	
	10	20	56	16	29	23	29	57	0
	17	24	48	24	42	23	43	57	
	24	20	48	24	29	23	43	43	–
Mar.	3	28	40	28	33	18	29	43	
	10	36	24	40	38	18	29	29	
	17	32	24	40	38	32	57		0
	24	24	24	40	33	32	57		
	31	24	24	44	29	46	43	29	–
Apr.	7	24	16	44	17	41	14	14	
	14	48	16	24	17	27			8
	21	68	12	8	17	23			
	28	72	8	8	8	27			
May	5	68	8	8	8	27			
	12	72	4	8	4	27			165
	19	72	4	4	4	23		14	
	26	64		4	8	18		14	–
June	2	56	8	4	13	18		29	
	9	44	4	4	8	14	29	14	
	16	44	4	4	8	14	14	14	259
	23	40			4	14	29	14	–
July	23	16	20		25	9	14	43	149

collectively, any significant concordance of behaviour may be considered an expression of evolutionary modification, or restriction on immigration, that has been guided by the nature of the environment. Unless otherwise indicated, the following topics refer to the twenty-five species of upland trees.

Leaf production (flushing)

Young leaves are being expanded throughout the year except during a short period centering on the first week in January, which is about one-third through the long dry season and before the soil profile has been exhausted of its readily available water at any depth (Table 4). Later in the year a similar group response to a milder dryness is reflected in a proportionate reduction of activity during the 'veranillo', a local term useful for designating the brief period centered in late July when rainfall is regularly less plentiful.

It is notable that in 1970 no effective rains fell until mid-May, yet approximately 70% of the trees flushed in the last 10 days of April, well before the dwindling supplies of readily available soil moisture below 30 cm were replenished. All of the twenty-five species participated in the major flush of activity that followed the major dry period, but only half flushed again following the veranillo.

Since a considerable number of species put out new leaves well in advance of the rainy season, this seems clear evidence that deficient soil moisture had not been a force necessitating leaf cast earlier in the dry season. Deciduous forests in the vicinity of Varanasi, India, also flush in the driest and warmest time of the year, well before the rains normally begin (Misra n.d.), and tropical grasses likewise put forth their new leaves well before the start of a new rainy season (Daubenmire 1971). Walter (1968) attributes this pre-rain flushing to the triggering effect of rising temperatures, but the monthly temperature data for Cañas (Table 1) provide no rational explanation as to why flushing should start about 1 February and reach the climax of this activity about 1 May. However, at the latitude of Cañas, 10° 28′N, there is an annual variation in length of day of approximately 1 h 12 min (List 1951) and this seems a more likely triggering mechanism. Njoku (1964) has shown experimentally that daylength control over phenology is important at 10° latitude in Africa, and Lawton & Akpan (1968) provide evidence of its effectivity at 7° 26′.

With flushing spread over 11 months, and 3 months elapsing between the start of flushing and attainment of maximum activity, it is strikingly evident that tropical dry climates exert far less control over flushing than the cold winters of temperate latitudes.

Leaf senescence

The percentage of species casting their leaves at the same time (Table 4) reaches its peak exactly coincident with the middle of the dry season, with this activity then largely suspended during the pre-veranillo rains, and completely suspended during the post-veranillo rains.

Most of the trees that stand leafless for a time, which is slightly less than half the upland group of twenty-five species, are in this condition late in the dry season.

An appreciable number of trees retain at least some leaves the year around after the plants reach maturity, with understorey shrubs and tree seedlings showing even stronger tendencies toward evergreenness. This forest is therefore properly referred to as semi-deciduous.

The fact that 56% of the upland trees retained active leaves through even the most severe part of the dry season shows that the degree of dryness at Cañas is certainly less absolute as a restriction on the persistence of membranous leaves than the regular periods of freezing weather in the Ohio Valley, U.S.A. Perhaps nothing points this up better than the observation that whereas *Cochlospermum vitifolium* dropped its leaves at the start of the dry season, and then put forth new ones when the rains returned (Fig. 6b), *Jacquinia aurantiaca* Ait., rooted in the same soil, lost its leaves gradually during the rainy season, and then flushed at the start of the dry season!

In temperate latitudes leaves are almost invariably cast as days are shortening, and for several species it has been demonstrated that the change in photoperiod is the triggering mechanism. At Cañas senescence in some species began while the days were shortening, but even more species started leaf drop after the solstice with the peak of this activity a month past that date.

Senescence and abscission are consequently attuned more closely to dryness than daylength, with major and minor peaks of these phenomena correlating closely with major and minor peaks of dryness.

Flowering

When pollination is used as a rigorous criterion of flowering, this activity has a bimodal distribution over the year, with most trees flowering during a protracted period centered about two-thirds through the dry season, and a smaller group flowering during the veranillo (Table 4). The lagging response to the onset or even the centre of the dry season may indicate that flower initials are not formed until the onset of dry weather, with several months then required for the development of floral organs.

The peak of flowering coincides fairly well with the period when the canopy is most nearly leafless, and since these trees are nearly all insect pollinated there may well be an advantage to the coincidence of flowering and leaflessness with regard to the visibility of flowers and ready access to them during the time of year when bees are most active (Janzen 1967).

That flowering can be successful in the rainy season too is shown by *Lysiloma, Chomelia* and *Sweetia panamensis* Benth. which flowered only in the rainy season, yet set abundant crops of seeds. Also seventeen species of trees, not all of which are included in Table 3, were observed to have two or more bursts of flowering during the year's observations, with at least one burst in the rainy season.

The flowering season of these trees growing at low altitude in a dry climate coincides closely with Allen's data for trees at low altitude but in a wetter climate about Golfo Dulce, Costa Rica, as summarized by Janzen (1967), but contrasts with the bimodal (February and April) flowering curve (Fournier & Salas 1966) for trees in the cooler and wetter climates of the mountains a few kilometres west of San José.

According to Walter (1964), flowering in tropical semi-deciduous forest usually reaches its peak just prior to the advent of rains, and coincides with the production of new leaves. Pooled data of the present study show that the peak of flowering came about 2 months before the normal advent of rains, with flushing not reaching its peak until the rains began. When individual trees are considered, flowering was always in advance of flushing and separated by 1–6 months, during which both activities were suspended.

Frequently flowering and leafing are clearly antithetic, especially when only a part of the canopy of a tree will shed its leaves and then flower, with the remaining part retaining foliage throughout. When each tree is considered as an individual, however, flowering and photosynthetic activity are seldom antithetic. Only in *Bombacopsis, Cochlospermum* and *Piscidia* was flowering restricted to a period when the entire canopy stood leafless. In ten out of the twenty-five species new leaves were expanding while pollination was in progress.

Alvim (1964) has suggested that any antithesis between vegetative and sexual activity may result from internal competition among the plant's organs for metabolites and/or hormones. Janzen (1967) argued that this alternation of flowering and vegetative activity is advantageous because rapid growth at the start of the rainy season is essential if a plant is not to be overwhelmed by the new growth put on by its neighbours. Accordingly at this season all energy must be channelled into new growth at the expense of flowering. This adaptational interpretation of alternating sexual and vegetative phases may be appropriate for most trees of the dry forest, but it seems peculiarly inapplicable to those in which the antithetic behaviour involves only well-defined sectors of the same canopy (e.g. *Dalbergia*, *Manilkara*, *Schizolobium parahybum* (Vell.) Blake, *Tabebuia palmeri* Rose, *Trichilia tomentosa* HBK., and five more species listed by Janzen).

Those tropical trees in which the canopy becomes sharply partitioned into flowering and vegetative sectors pose an interesting situation for consideration with regard to the theory that florigens produced in one part of a shoot migrate to other parts where they trigger flowering.

Table 5. *Comparison of pollen and disseminule vectors in tropical and temperate forests (the Ohio data are based on a sample of thirty species; the Indiana and Costa Rica data represent twenty-five species in each location; the number of species considered in the Venezuela forest was not specified)*

	Vector percentages			
	Pollination		Dissemination	
	Animal	Wind	Animal	Wind
Temperate deciduous forest				
Indiana	28	72	64	32
Ohio	17	83	67	33
Tropical semi-deciduous forest				
Costa Rica	96	4	48	52
Tropical deciduous forest				
Venezuela	–	–	27	73

Some interesting contrasts are revealed by comparing pollination vectors in the deciduous forests of tropical and temperate latitudes. To obtain an objective sample of canopy trees representative of the Ohio Valley (U.S.A.) forests, species lists have been combined from studies in Indiana by Keller (1946) and by Potzger, Friesner & Keller (1942). This provides a total of twenty-five upper canopy species to compare with the twenty-five upland trees of the Cañas area. As a check, the thirty trees listed by Braun (1936) in a study of a forest in Ohio (U.S.A.) have also been considered.

In Table 5 it is clear that in the tropical semi-deciduous forest pollination is almost entirely by animals (mainly bees), whereas in the temperate deciduous forests wind is the usual agent. Since pollination is attuned to the leafless or nearly leafless condition in both forest regions, whereas the major vector is wind in the one instance and insects in the other, the timing seems directed more toward minimizing leaf interference with wind or insects rather than toward favouring a particular vector. This leaves the question of why different vectors have been favoured unanswered.

Wind pollination and the deciduous habit probably did not evolve in response to a similar environmental complex as Whitehead (1969) has suggested, for the drought-deciduous forest combines deciduousness with entomophily, whereas the winter-deciduous forest combines deciduousness with anemophily.

Whitehead (1969) further states that the activity of insect pollinators is relatively low during the dry season in drought-deciduous forests, whereas the reverse is true of bees, which are efficient pollinators (Janzen 1967). Furthermore, Whitehead reasoned that in drought-deciduous forest, since the 'understorey remains evergreen . . . wind velocities within the forest would remain low' and, therefore, wind would be less reliable as a pollen vector than insects. But this deduction has a faulty base. Despite the strong tendency toward evergreenness among shrubs and tree seedlings, winds are strong enough during the dry season that the leaves are wind-rowed, collecting in depressions and about obstructions leaving intervening areas of the forest floor swept bare. This is not only true of Guanacaste, but has been reported elsewhere in tropical deciduous forest. Thus the prevalence of entomophily cannot be attributed even in part to a lack of sufficient wind to keep pollen in suspension.

A highly potent situation that probably favours entomophily in dry-season deciduous forest is the high species diversity. While the flora is definitely not as rich as rainforest, it is clearly more diversified than winter-deciduous forest. Wind disseminated pollen loses its effectivity exponentially with increasing distance from the source, but an insect with its entire pollen load travels considerable distances (up to 8 km in honeybee) going directly from one tree to another of a species providing desirable nectar or pollen. Thus high diversity that results in wide spacing of the individuals or families of each species of tree may well have favoured flowering at a season when flowers can be seen from the greatest distance by insects that locate flowers by sight. In tropical rainforest where there is no favoured season with respect to leaf cast, there is no season of better visibility to be exploited.

A hypothesis that the insect fauna of temperate forests has been quantitatively or qualitatively inadequate, and so favoured anemophily by default is not to be countenanced, for there is an appreciable number of secondary trees in the winter-deciduous forest that depend on insects (*Acer*, *Aesculus*, *Amelanchier*, *Asimina*, *Catalpa*, *Cercis*, *Cornus*, *Crataegus*, *Diospyros*, *Gleditsia*, *Gymnocladus*, *Halesia*, *Liriodendron*, *Magnolia*, *Malus*, *Oxydendrum*, *Prunus*, *Pyrus*, *Robinia*, *Salix*, *Tilia*, etc.), and these set good crops of seed as regularly as the anemophilous trees that dominate (*Acer*, *Carpinus*, *Carya*, *Castanea*, *Fagus*, *Fraxinus*, *Quercus*, *Ulmus*, etc.). The prevalence of entomophily in the extratropical forest may in fact represent only an accident occasioned by circumstances that made the few but taxonomically rich families Betulaceae, Fagaceae, Juglandaceae, Salicaceae, and Ulmaceae, all of which are mainly anemophilous, especially at home in these climates.

Dissemination

Among the upland trees dissemination is spread over most of the year, as is pollination (Table 4). But whereas the peak period of dissemination coincides fairly closely with the peak period of pollination (with a small lag), there is no secondary increase of dissemination activity during the veranillo such as shows up in the pollination record. If disseminules retain viability for only a short time after they are cast, it is not difficult to see the strategy of concentrating dissemination in a period just prior to the rainy season, thus making the long stretch of moist conditions fully available for seedling establishment, whereas dissemination during the veranillo would allow considerably less time for germination and establishment, unless viability was retained and predation escaped for the next three-quarters of a year.

Whereas dissemination in drought-deciduous trees is mainly just before the start of the growing season, in winter-deciduous forest it is mainly at the end of the growing season.

Among the twenty-two upland forest trees which both pollinated and disseminated during the year of study, the average time elapsing between the start of these sequential functions was 3·5 months.

Janzen (1967) feels that in the dry tropics selection favours pollination and fruit development during the season of low rainfall since the terrestrial animals that do not aestivate or emigrate during this season must depend heavily on nectar or fruit juices as a source of moisture. Thus pollination and dissemination services are performed more thoroughly. Furthermore, bees are more active during the dry season, although cause and effect are not easily distinguished here.

Since the dissemination peak is coincident with the time of maximum leaflessness—and most trees are wind disseminated—this timing is advantageous in that foliage interferes least with the scattering of anemochores, as well as the success of animals in locating fruits.

Dissemination among the upland trees at Cañas is accomplished equally by wind and by animals, whereas in the temperate zone homologue animal dissemination clearly prevails (Table 5). Temperate deciduous forests are characterized by climates where winds are not a conspicuous feature, but, as pointed out above, the climates of tropical semi-deciduous forests have much wind during the dry season, and the emphasis on wind dissemination seems an evident response to the availability of abundant wind energy at this season. Aristeguieta (1968) reports that the majority of the (wholly!) deciduous forest species of Venezuela are wind disseminated, which is even more of a contrast with the temperate zone trees (Table 5).

Radial changes in tree trunks in relation to other phenology

In twelve of the twenty-five upland forest species growth was confined to the rainy season, frequently coinciding rather closely with its duration (Figs. 1–14): *Bursera, Chlorophora, Cordia alliodora, Dalbergia, Enterolobium, Godmania, Guazuma, Guettarda, Luehea, Platymiscium, Tabebuia* and *Sapranthus*. Thirteen species continued growth for varying periods of a month or more into the dry season: *Bombacopsis, Chomelia, Cordia stellifera, Lonchocarpus, Luehea, Lysiloma, Machaerium, Manilkara, Piscidia, Pterocarpus, Spondias purpurea, Sterculia* and *Trichilia*. Both groups contain species that showed strong shrinkage during the dry season, with others shrinking little if at all.

Among the three species represented in both upland and riparian habitats (*Enterolobium, Spondias purpurea* and *Tabebuia*), the upland member showed the greater development of a water deficit.

It is noteworthy that complete divestment of leaves gave no special protection against tissue dehydration, as shown by the dry-season shrinkage of *Bombacopsis, Chomelia, Cochlospermum, Guettarda, Luehea* and *Tabebuia*.

Five species showed phenomenal dry season shrinkage that amounted to more than the net annual increment: *Bursera, Calycophyllum, Chomelia, Sapranthus* and *Swietenia*. Two of these (*Calycophyllum* and *Swietenia*) grew along the river where their roots were in continuously moist alluvial sand. Among the temperate zone trees studied by Daubenmire & Deters (1947) only *Robinia pseudoacacia* L. gave a similar strong response to protracted drought. In all such trees this shrinkage must be taken into account when measurements are made annually for the purpose of monitoring growth in forest stands.

Of the only two upland species that retained fully mature and healthy leaves throughout the year (*Machaerium* and *Manilkara*), the stem of the former shrank considerably, but of the latter very little. Of those that always supported either mature or expanding foliage (*Enterolobium*, *Guazuma*, *Pterocarpus* and *Trichilia*), shrinkage also varied from negligible to pronounced.

As pointed out earlier, a considerable number of trees put forth new leaves before the dry season ended. In most of these (*Bursera*, *Chomelia*, *Cochlospermum*, *Cordia alliodora*, *Dalbergia*, *Enterolobium*, *Godmania*, *Guettarda*, *Lonchocarpus*, *Luehea*, *Sapranthus*, *Spondias purpurea*, *Tabebuia* and *Trichilia*) leafing was accompanied by pronounced shrinkage in such a manner as to indicate that heavy demands were being made on the water supply by blades with minimal cutinization.

Also, leaves of some precocious species (e.g. *Erythroxylon havanense* Jacq.) partly wilted as they approached full size, hanging in a conspicuously limp condition until the first heavy rainfall of 16–17 May. In *Piscidia* new pinnae had barely started to expand on 21 April, and after they were only a few millimetres long further growth ceased entirely until after the first rain.

In twelve species flowering was active during at least part of the major period of trunk shrinkage. Thus both flowering and flushing seem inhibited to a negligible degree by drought that is severe enough to cause marked dehydration of the trunk tissues!

Rain gauges near the forest stand (the source of the data in Fig. 14c) and 1·8 km distant did not yield similar data regarding the distribution of showers at the end of the dry season, showing that areal distribution was far from uniform. Thus the violent fluctuations in radius at that season are not closely correlated with the rainfall records in Fig. 14(c). However, it is fairly certain that the showers which apparently resulted in temporary radial increases all yielded too little water to have wet the soil more than a few centimetres at most. The stimulus must have resulted from either a temporary suspension of transpiration making soil moisture more effective, or from water taken in by twigs and such foliar or reproductive organs as they bore.

FIGS. 1–14. Percentage distribution of net annual radial change in tree trunks as measured weekly. Broken segments of the line represent the period during which weekly details of change were not recorded. Phenologic symbols across the top of the graphs show other conditions of the trees at the dates of measurement: open transverse bar—young leaves being expanded; filled transverse bar—mature, healthy leaves present; short vertical lines—leaves discolouring or dropping while green, due to internal causes; rows of dots—pollination in progress; open circles—pollination finished, but dissemination not yet begun; filled circles—dissemination in progress.

Anacardium excelsum Fig. 7b
Bombacopsis quinata Fig. 11c
Bursera simaruba Fig. 1a
Calycophyllum candidissimum Fig. 2a
Ceiba pentandra Fig. 2c
Chlorophora tinctoria Fig. 5c
Chomelia spinosa Fig. 3a
Coccoloba caracasana Fig. 12b
Cochlospermum vitifolium Fig. 6b
Cordia alliodora Fig. 4a
C. stellifera Fig. 4b
Dalbergia hypoleuca Fig. 5a
Enterolobium cyclocarpum Fig. 8b, c
Godmania aesculifolia Fig. 4c
Guazuma tomentosa Fig. 3b
Guettarda macrosperma Fig. 6a
Hymenaea courbaril Fig. 7a
Inga spuria Fig. 2b
Licania arborea Fig. 7c
Lonchocarpus minimiflorus Fig. 5b
Luehea candida Fig. 1c
Lysiloma sp. Fig. 9b
Machaerium biovulatum Fig. 8a
Manilkara spectabilis Fig. 1b
Piscidia carthagenensis Fig. 3c
Platymiscium dimorphandrum Fig. 9c
Pterocarpus hayesii Fig. 14a
Sapranthus palanga Fig. 9a
Sloanea terniflora Fig. 12c
Spondias mombin Fig. 10c
S. purpurea Fig. 10a, b
Sterculia apetala Fig. 11a, b
Swietenia macrophylla Fig. 12a
Tabebuia neochrysantha Fig. 13a, b, c
Tectona grandis Fig. 14b
Trichilia colimana Fig. 6c

FIG. 14(c). Records of rainfall near the forest stand.

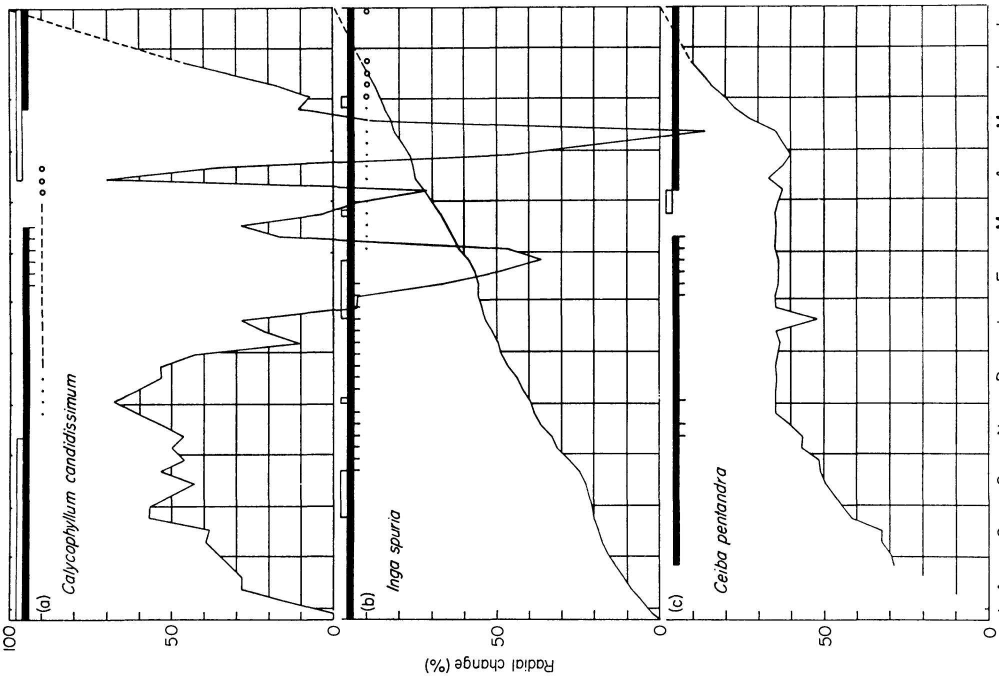

(a) Calycophyllum candidissimum
(b) Inga spuria
(c) Ceiba pentandra
Radial change (%)
100
50
0
J A S O N D J F M A M J J

FIG. 2.

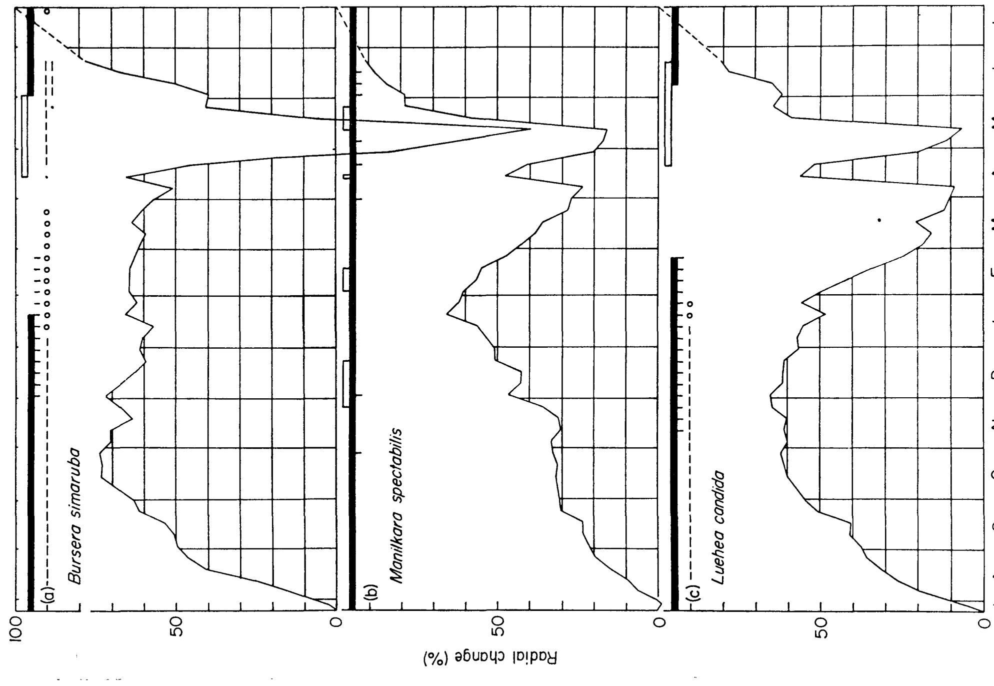
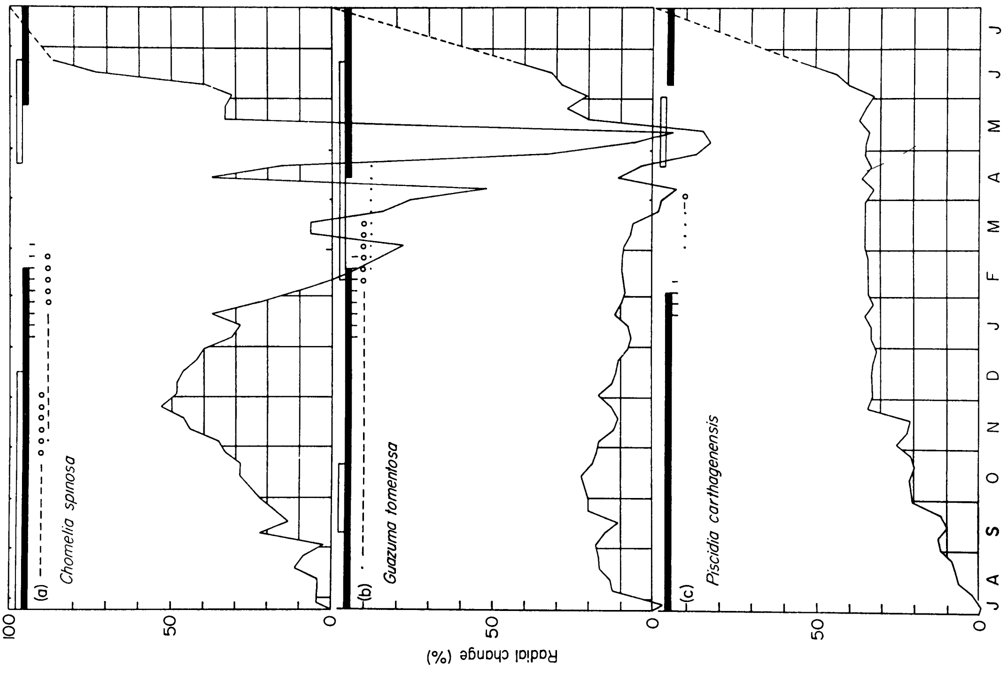
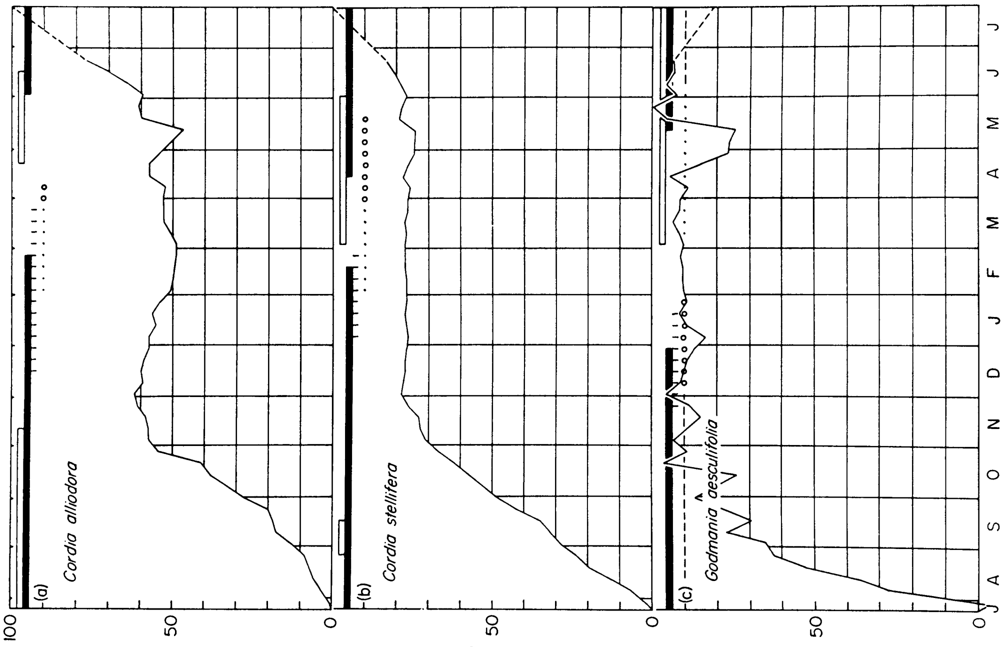

(a) Bursera simaruba
(b) Manilkara spectabilis
(c) Luehea candida
Radial change (%)
100
50
0
J A S O N D J F M A M J J

FIG. 1.



Radial change (%)
100
50
0
(a)
Chomelia spinosa
(b)
Guazuma tomentosa
(c)
Piscidia carthagenensis
J A S O N D J F M A M J J

FIG. 3.



Radial change (%)
100
50
0
(a)
Cordia alliodora
(b)
Cordia stellifera
(c)
Godmania aesculifolia
J A S O N D J F M A M J J

FIG. 4.

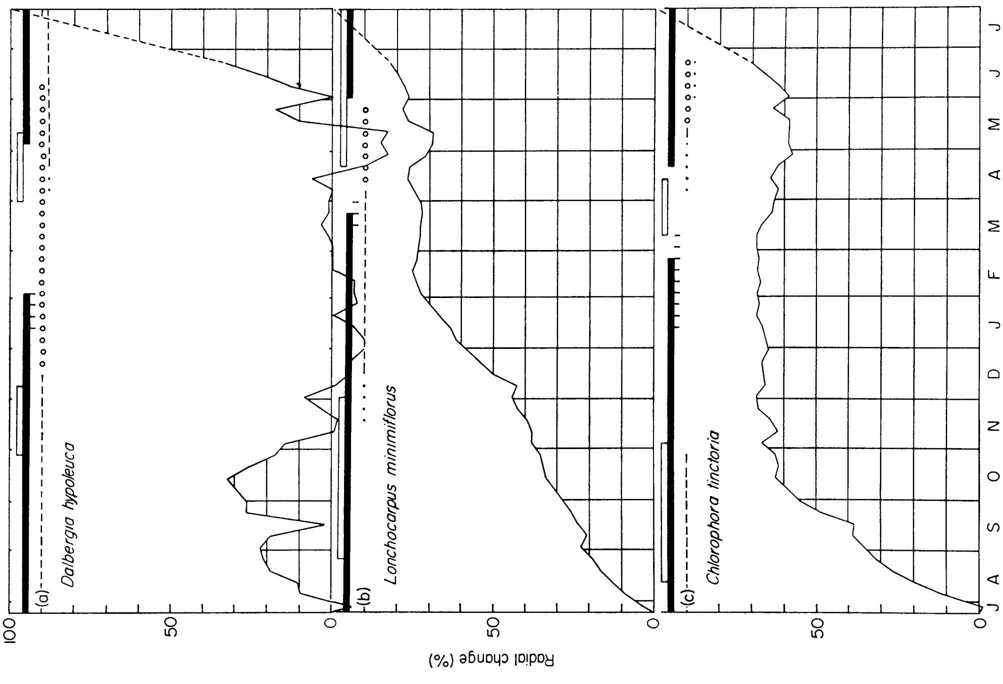

(a)
Dalbergia hypoleuca
(b)
Lonchocarpus minimiflorus
(c)
Chlorophora tinctoria
100
50
0
50
0
50
0
Radial change (%)
J A S O N D J F M A M J J

FIG. 5.

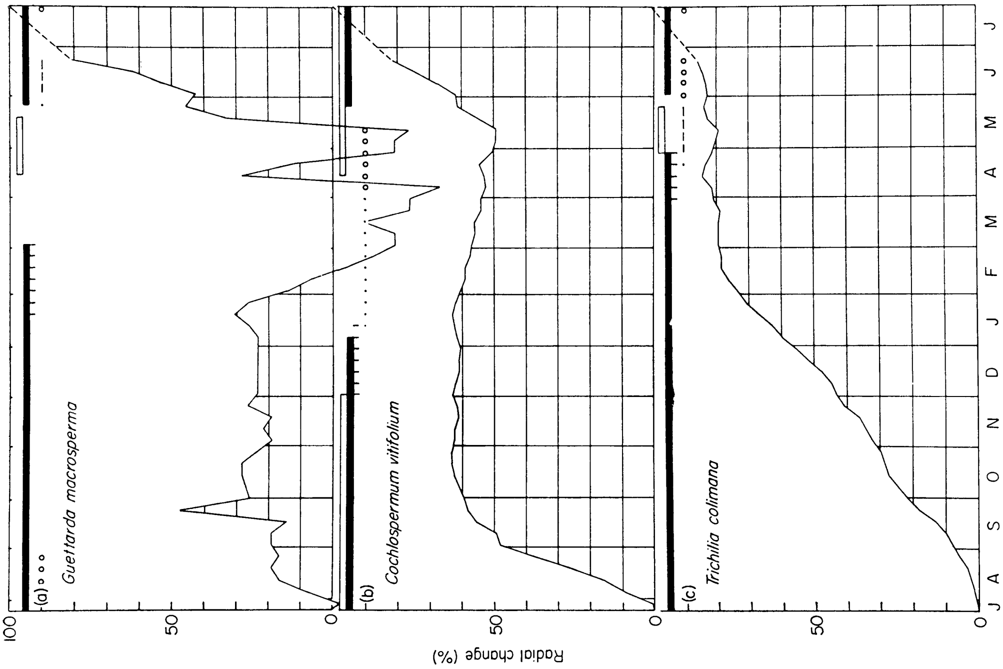

(a)
Guettarda macrosperma
(b)
Cochlospermum vitifolium
(c)
Trichilia colimana
100
50
0
50
0
50
0
Radial change (%)
J A S O N D J F M A M J J

FIG. 6.

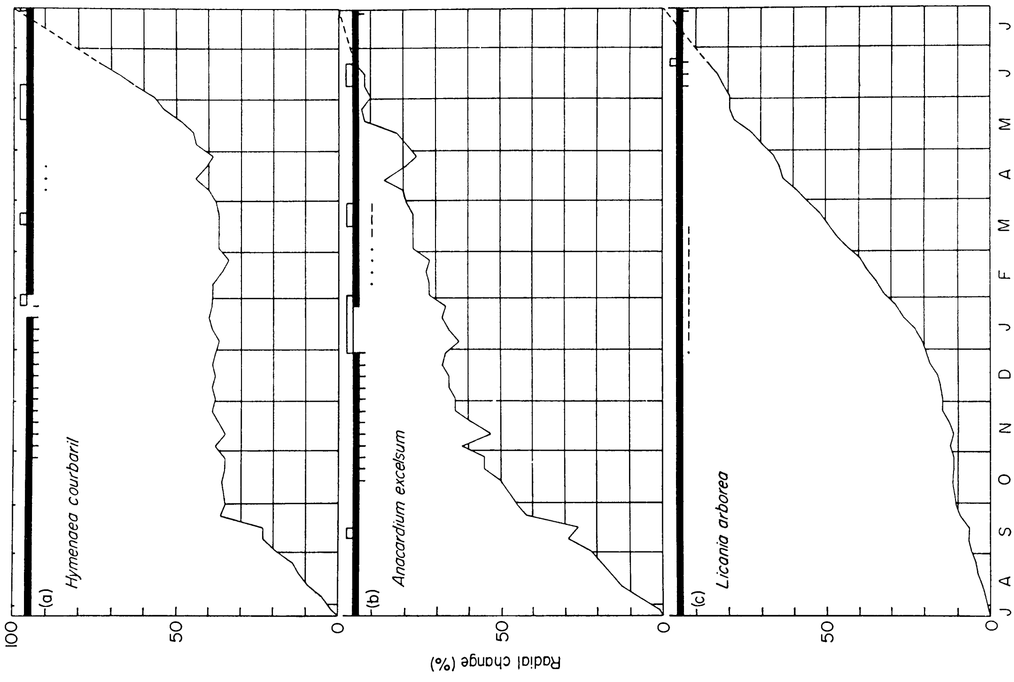

(a) Hymenaea courbaril
(b) Anacardium excelsum
(c) Licania arborea
Radial change (%)
100
50
0
J A S O N D J F M A M J J

FIG. 7.

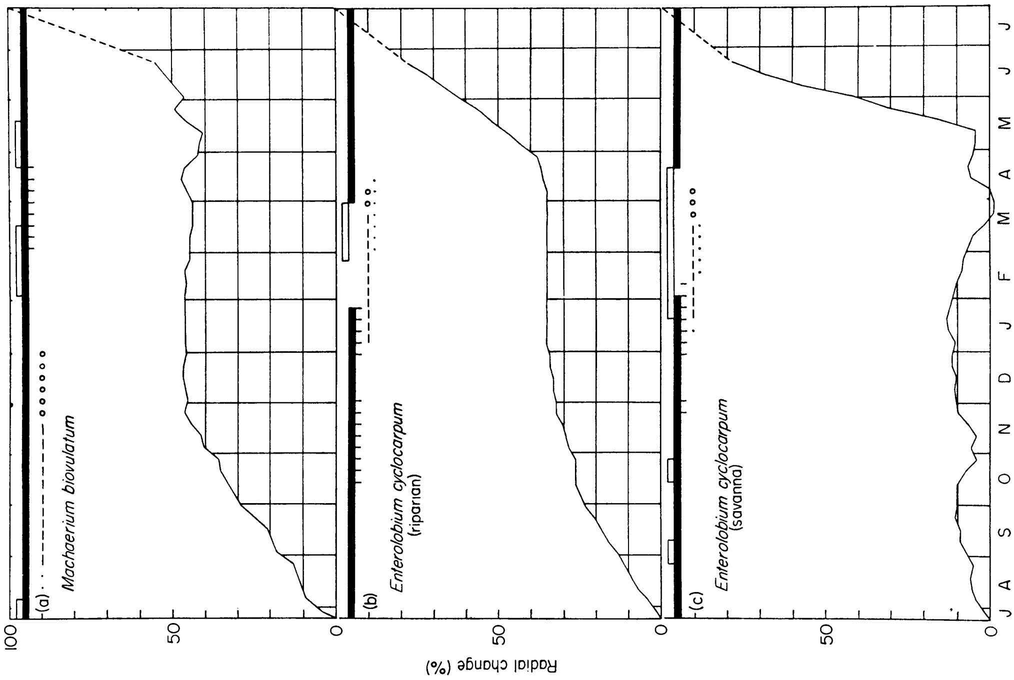

(a) Machaerium biovulatum
(b) Enterolobium cyclocarpum (riparian)
(c) Enterolobium cyclocarpum (savanna)
Radial change (%)
100
50
0
J A S O N D J F M A M J J

FIG. 8.

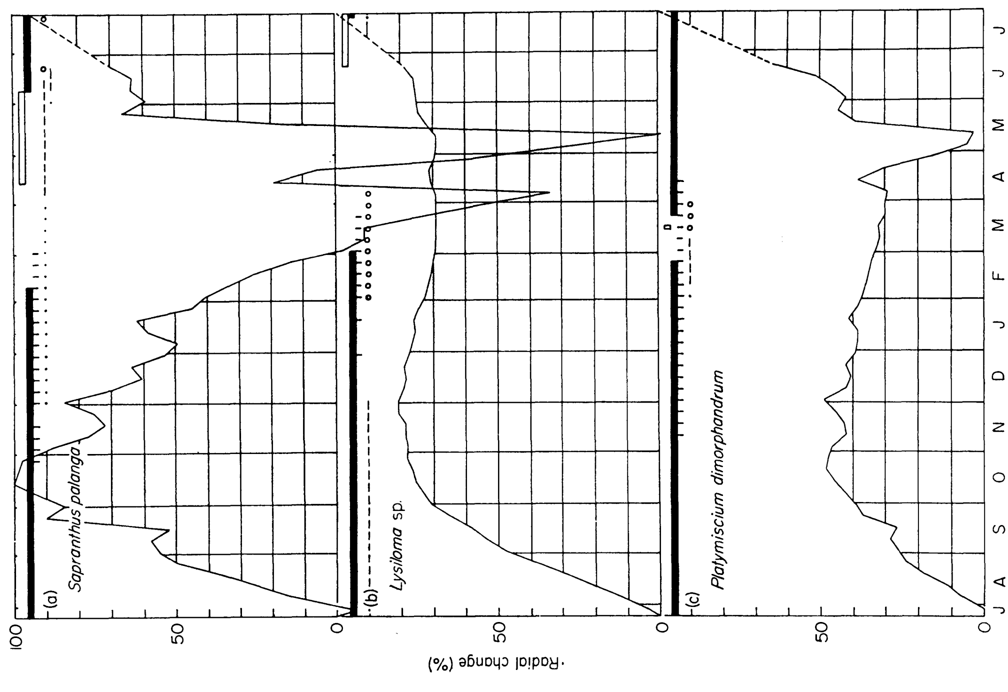

(a) Sapranthus palanga
(b) Lysiloma sp.
(c) Platymiscium dimorphandrum
Radial change (%)
100
50
0
50
0
50
0
J A S O N D J F M A M J J

FIG. 9.

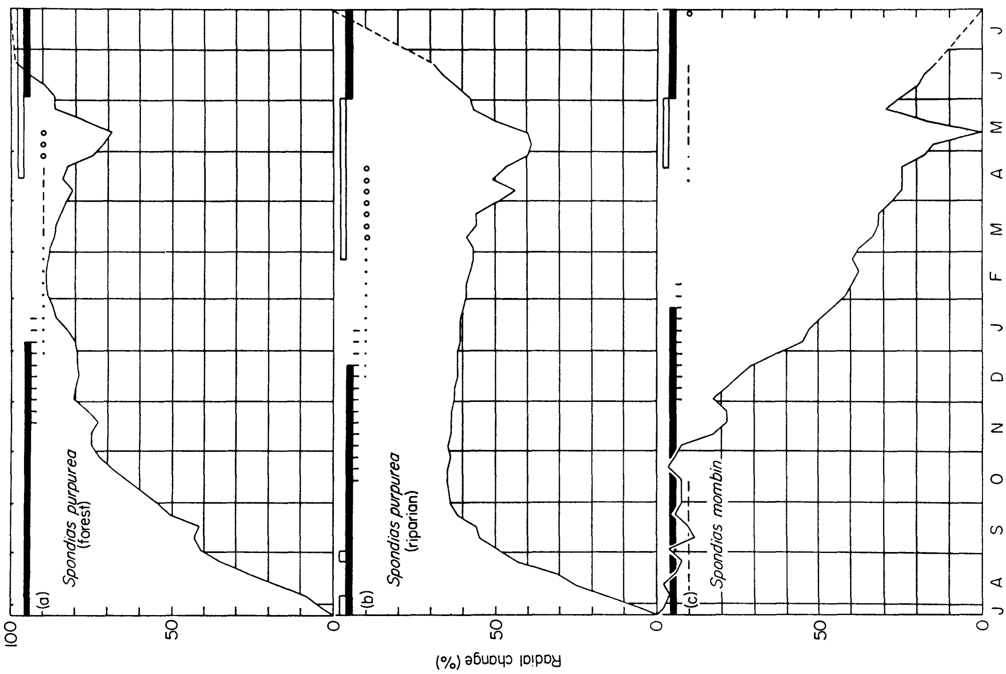

(a) Spondias purpurea (forest)
(b) Spondias purpurea (riparian)
(c) Spondias mombin
Radial change (%)
100
50
0
50
0
50
0
J A S O N D J F M A M J J

FIG. 10.

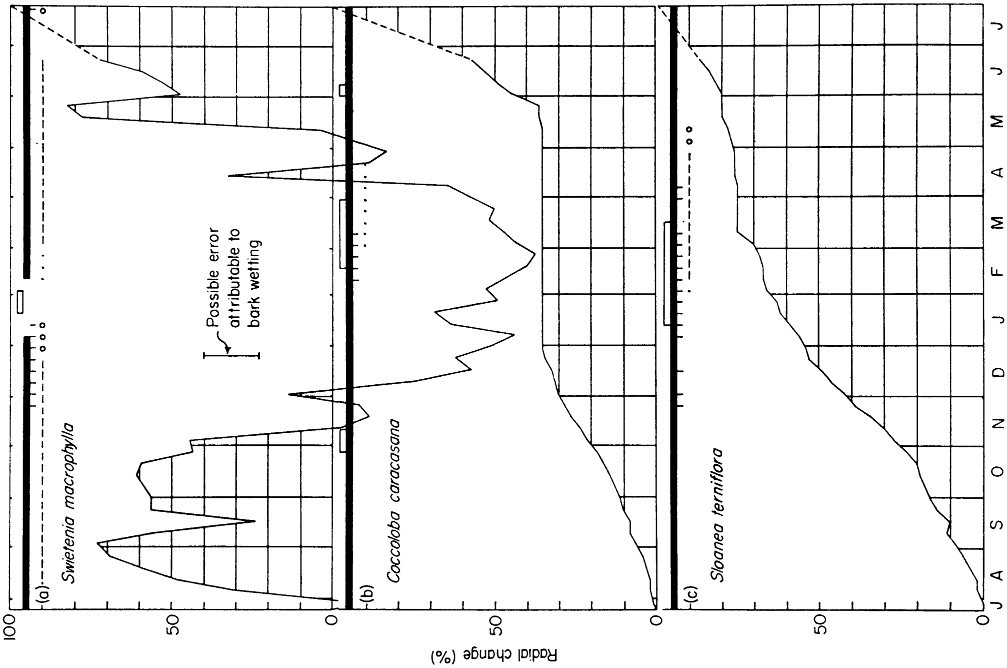

Radial change (%)
100
50
0
50
0
50
0
(a) Swietenia macrophylla
Possible error attributable to bark wetting
(b) Coccoloba caracasana
(c) Sloanea terniflora
J A S O N D J F M A M J J

FIG. 12.

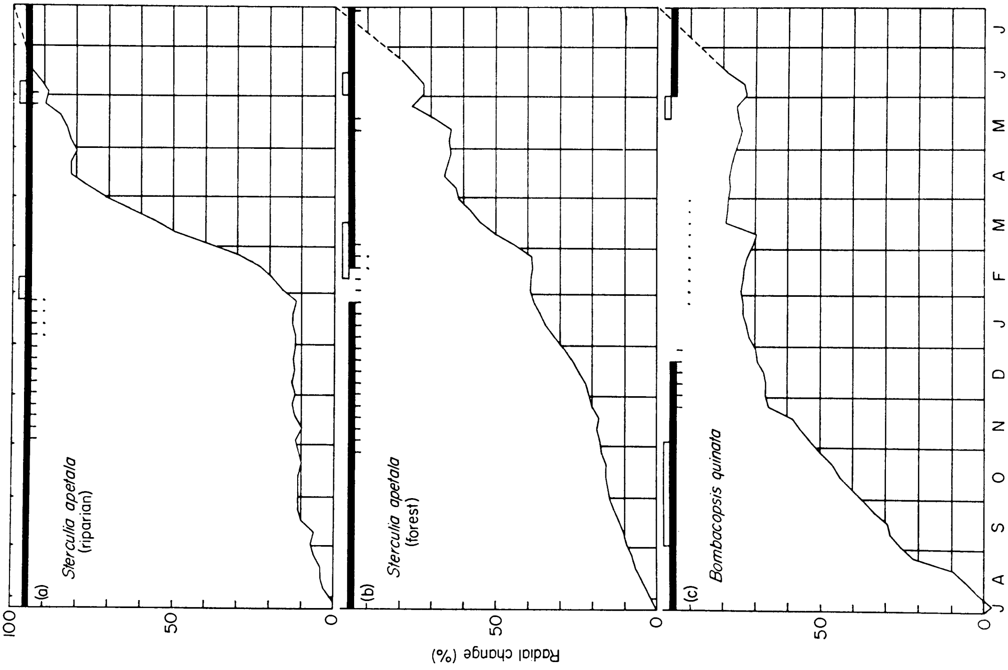

Radial change (%)
100
50
0
50
0
50
0
(a) Sterculia apetala (riparian)
(b) Sterculia apetala (forest)
(c) Bombacopsis quinata
J A S O N D J F M A M J J

FIG. 11.

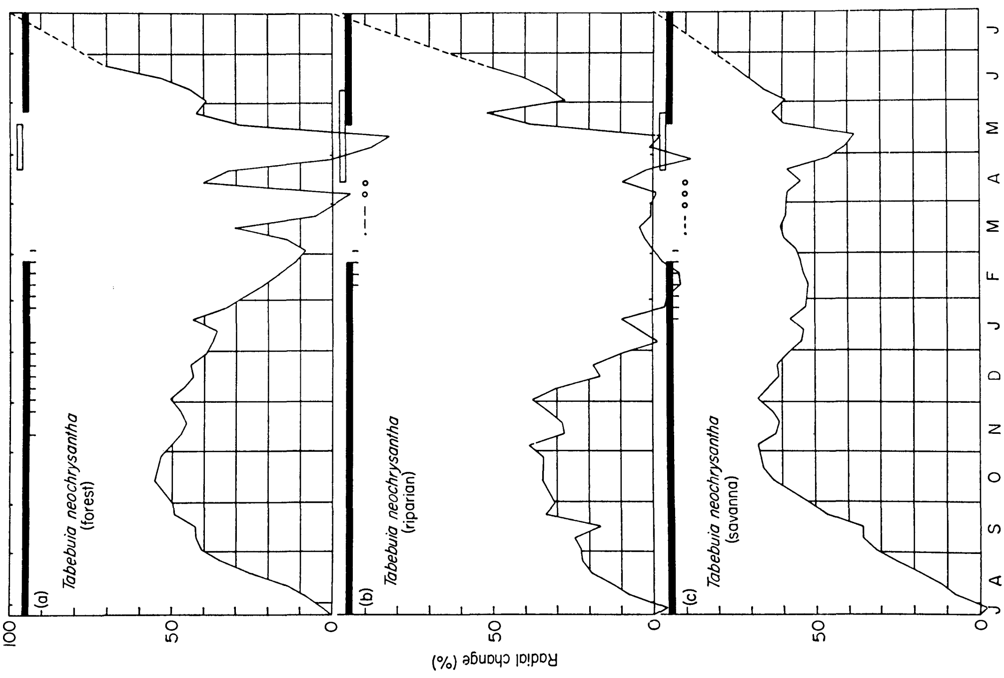

(a)
Tabebuia neochrysantha (forest)
(b)
Tabebuia neochrysantha (riparian)
(c)
Tabebuia neochrysantha (savanna)
100
50
0
Radial change (%)
J A S O N D J F M A M J J

FIG. 13.

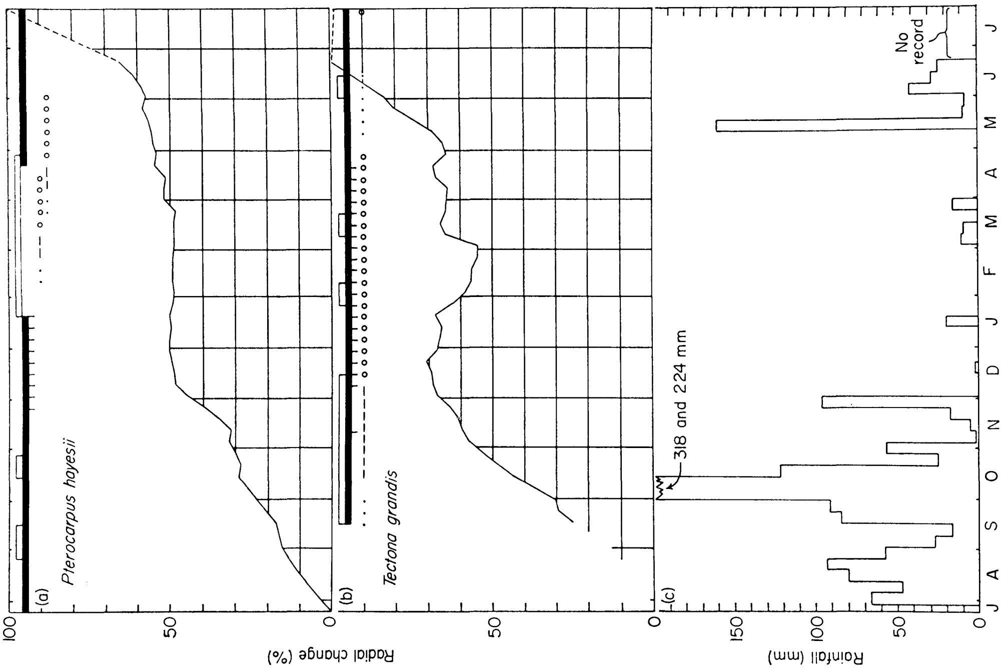

(a)
Pterocarpus hayesii
(b)
Tectona grandis
(c)
318 and 224 mm
No record
100
50
0
Radial change (%)
150
100
50
0
Rainfall (mm)
J A S O N D J F M A M J J

FIG. 14.

Alvim (1964) has observed that the cambium of tropical trees remains inactive until after new leaves start to unfold, and this was true at Cañas. However, it seems unlikely that the cambial stimulus resulted from hormones released when active growth was resumed at the twig apices, since the inception of radial growth was delayed weeks or months after flushing, and brief episodes of flushing were not regularly followed by increased cambial activity. For example, in *Hymenaea* and *Tectona* there were two brief flushes during the period of dry-season quiescence, with neither being followed by renewed diameter increase. In some of the other species (*Ceiba*, *Chlorophora*, *Enterolobium* (riparian individual), *Godmania*, *Machaerium* and *Platymiscium*) there was a delay between the start of flushing and the start of radial increase of 1·5–4·0 months.

Group characteristics of obligative phreatophytes

Any interpretation of group behaviour and its adaptive significance among obligative phreatophytes must be quite tentative since only seven of the riparian trees that were selected for study seem to be essentially restricted to soils where the water table is within rooting depth, insofar as ecologic relations of the trees were observed in the Cañas area. Six of these seven phreatophytes retained leaves throughout the year, and only one stood leafless for a short time. Thus even the group of seven species reflects a general impression that subirrigated forests in the Cañas area are predominantly evergreen, and indicates that the group, though small, may be representative.

As on the uplands, pollination in these trees is centered in the dry season. Since the forest as a whole is evergreen, the prevalence of dry-season pollination probably reflects adaptation to the seasonal activity of Hymenoptera with clear implication that the visibility of flowers has not been of primary importance in directing evolutionary emphasis on dry-season flowering.

There are frequent reports in the literature that the same species of tree may remain evergreen in ever-wet climates, but lose its leaves regularly in climates with a pronounced dry season. None of the group of seven facultative phreatophytes studied showed this behaviour, so it must be concluded that their deciduousness is either genetically fixed or a much wetter climate is needed for this adaptation to reveal itself.

In Table 3 all native trees have been classified with respect to their habitat of occurrence and the maximum shrinkage observed during the dry season. This arrangement shows that the species which appear to be phreatophytes in this climate shrink very little during the dry season, whereas species growing in the same environment, but equally capable of growing away from the influence of a water table, nearly all shrank markedly regardless of whether soil moisture supplies were plentiful or limited.

Capacity for rapid cambial growth

Data available for the trees studied by Daubenmire & Deters (1947) at Moscow, Idaho (U.S.A.), permit comparison of diameter growth rates between temperate zone trees and those of the Cañas area. Although no records were kept of the diameters of the individuals, in both groups the size ranged between approximately 10–50 cm (dbh), with most individuals falling well within the extremes.

By all criteria of comparison, maximum growth rates are higher in trees native to areas where the unfavourable season is cold, in comparison with those growing where the unfavourable season is dry (Table 6). In both climates evergreen species tend to have a lower capacity for rapid growth.

The degree to which diameter growth is confined to a narrow span of months is much more absolute where quiescence is correlated with a cold season (Daubenmire & Deters 1947) than where it is correlated with a dry season. However, the more rapid growth rate and shorter period of activity at high latitudes cannot be interpreted as a consequence of adaptation to a short frost-free season, for all of the trees included in the high latitude group start diameter growth long before the average date of the last frost in spring, and then cease growth in mid-summer.

Table 6. *Maximal radial increment (in* 0·001 *inch,* 0·025 *mm) in any* 4-*week period*

	Costa Rica			Idaho	
	All 25 species	Species (8) never leafless*	Always with healthy leaves	All 17 species	Evergreen (8) species
Lowest	13·2	14·9	13·2	19·0	20·7
Mean	30·7	27·6	–	44·6	34·1
Median	26·7	25·6	–	40·5	34·4
Highest	59·9	41·0	14·9	81·5	47·5

* In some of these, senescing leaves persisted until new leaves started to unfold, but the two individuals that qualify for the next column retained mature and healthy leaves the year around, as do the 'evergreen' species in the Idaho column.

Distinctiveness of xylem layers

Nearly all trees of extratropical regions add a morphologically distinct xylem layer to their woody cylinder each year. Coster (1927) and Alvim (1964) state that the interruption of cambial activity in tropical trees also results in a discontinuity between adjacent annual increments. However, this is mostly untrue of the trees sampled in the Cañas area. All trees were not sampled (many resist an increment borer!) but, of those that stood leafless for a time, *Bombacopsis*, *Dalbergia* and *Spondias purpurea* showed no evident distinctions between adjacent xylem increments. *Bursera*, *Enterolobium* and *Tabebuia* showed exceedingly faint discontinuities, with only *Cordia alliodora* resembling temperate zone trees in having fairly distinct layers. *Cochlospermum* wood has many very narrow layers, obviously far too many for just one to have formed each growing season. The generalization is warranted for the Cañas area that although nearly all trees have a period when diameter growth comes to a complete halt, extremely few have wood with annual increments distinct enough to count or measure with confidence.

Comments on individual species

Spondias mombin was remarkable in that the diameter of the individual studied shrank progressively during the twelve months of study (Fig. 10c). The tree was a large handsome specimen, apparently in excellent health as it flowered and bore abundant fruit that the monkeys consumed without allowing any to mature. It grew on a river terrace with *Coccoloba* nearby on one side and *Anacardium* on the other, and neither of these trees showed abnormal behaviour. Both instruments on the *Spondias* reflected the shrinkage.

The phenology of *S. purpurea* was quite different in the two trees studied, the one on the upland and the other along the river (Fig. 10a, b).

Tabebuia neochrysantha showed most shrinkage where it grew in the upland forest, where competition from surrounding trees was greatest. This individual failed to flower and its leaf senescence began far ahead of the two other trees (Fig. 13). The riparian individual shrank more than the tree in the savanna where water was undoubtedly less abundant. Synchronous flowering of the upland and riparian individuals reflects the remarkably synchronous flowering of all trees of this species, and suggests that self-sterility is involved. Two other species of the genus grow in the area, but have very different flowering behaviour. *T. rosea* (Bertol.) DC. trees came into flower individually over a protracted period, whereas individuals of *T. palmeri* Rose had two bursts of flowering, these several weeks separated, and the population behaviour was not synchronized.

Sterculia apetala growing in the upland forest increased its diameter at almost a steady rate throughout the year, in contrast with interruptions suffered by all other trees in the same habitat (Fig. 11b). The individual on the river bank was unique in another way. It began active radial growth in the middle of the dry season, then became quiescent as rainfall became heaviest (Fig. 11a). Pollination, leaf senescence and flushing were not very closely synchronized in the two trees, but both had two leaf flushes.

Tectona grandis appears very well adapted to the Cañas environment (Fig. 14b). Except for flowering in the rainy season, and having two periods of successful flowering, its phenology is essentially modal with respect to the group of twenty-five native upland trees studied.

Lojab (1968) observed that in the ever-wet climate of Turrialba, Costa Rica, *Cordia alliodora* put on new radial growth very slowly from November to May, then continued growing at a moderately fast rate from June to October. The season of most active growth was the same at Cañas, but here there was gradual shrinkage during the dry season rather than gradual increase (Fig. 4a).

Also at Turrialba, Lojan (1968) found that the radii of *Bombacopsis quinata* remained stationary from November to May, then increased rather rapidly from June to October inclusive. At Cañas radial increase continued at the maximal rate to November, then slowly for two more months (Fig. 11c). Since the provenance of the Turrialba plantation is unknown, it is not clear whether the 3-month prolongation of cambial activity at Cañas is attributable to genetics or environment.

Holttum (1931) described the phenology of two trees of *Hymenaea courbaril* which had been planted in the ever-wet climate of Singapore. Those two individuals had quite different phenologies, and neither pattern matched the individual studied at Cañas (Fig. 7a). Thus there appears to be a wide range of genetic variation in this species corresponding with its wide geographic range from Mexico to the Antilles to South America.

ACKNOWLEDGMENTS

These studies were made while the writer was supported by a research grant from the National Research Foundation, U.S.A.

I am also indebted to Ing. Werner Hagnauer for permission to study trees on Hacienda La Pacifica, to Gary Hartschorn for making the records of 23 July 1970, and to Jean B. Daubenmire who helped with all the field work. The Costa Rican Ministerio de Agronomia y Ganaderia, upon the recommendation of Ing. Mauro Molina, contributed housing at the Estación Experimental Enrique Jimenez, convenient to the study sites. Dr William C. Burger kindly identified specimens of the trees, which are deposited in the Field Museum of Natural History, Chicago.

SUMMARY

In tropical deciduous trees in north-western Costa Rica leaf flushing is initiated during a

period when drought stress, to which it appears an adaptation, is reaching its peak of severity. In contrast with temperate zone trees, flushing is spread over about 11 months. Leaf senescence in the tropical forest seems more clearly triggered by drought stress than by daylength. For the forest as a whole there are two flowering seasons, a major and a minor, that correlate with major and minor seasons of drought. Tropical deciduous trees combine entomophily with deciduousness, this showing clearly that both characters did not evolve in response to the same aspect of environment. In the tropical trees dissemination is usually by wind and occurs at the end of the season of lowest vegetative activity, whereas in temperate zone trees dissemination is typically at the end of the vegetative season. In both the tropical and temperate trees, temporary dry-season shrinkage of the trunk varies from negligible in some species to shrinkage that exceeds the net annual increment in others. Dry-season shrinkage seems a genetic character of those tropical trees that have been compared in both upland and riparian habitats. Divestment of leaves gave no special insurance against trunk shrinkage during the dry season in the tropics. In the same trees both flowering and flushing occurred at times when trunk shrinkage indicated high moisture stress. In comparison with the tropical trees, radial growth of those in temperate latitudes is much more rapid and is confined to a shorter segment of the year. Despite pronounced seasonality of cambial activity in the tropical trees, the xylem of only one species showed fairly distinct annual layers.

REFERENCES

Alvim, P. de T. (1964). Tree growth and periodicity in tropical climates. *The Formation of Wood in Forest Trees* (Ed. by M. H. Zimmermann), pp. 479–95. Academic Press, New York.

Aristeguieta, L. (1968). El bosque caducifolio seco de los llanos altos centrales. *Boln Soc. venez. Cienc. nat.* **27**, 395–438.

Braun, E. Lucy (1936). Forests of the Illinoian Till Plain of south-eastern Ohio. *Ecol. Monogr.* **6**, 89–149.

Coster, C. (1927). Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. *Annls Jard. bot. Buitenz.* **37**, 49–160; **38**, 1–114.

Daubenmire, R. (1945). An improved type of precision dendrometer. *Ecology*, **26**, 97–8.

Daubenmire, R. (1971) Ecologic consequences of converting forest to savanna in north-western Costa Rica. (*In prep.*)

Daubenmire, R. (1972). Ecology of *Hyparrhenia rufa* in derived savanna in north-western Costa Rica. *J. appl. Ecol.* **9**, 11–23.

Daubenmire, R. & Deters, M. E. (1947). Comparative studies of growth in deciduous and evergreen trees. *Bot. Gaz.* **109**, 1–12.

Fournier, L. A. & Salas, S. (1966). Algunas observaciones sobre la dinámica de la floración en el bosque tropical húmedo de Villa Colon. *Revta Biol. trop.* **14**, 75–85.

Holttum, R. E. (1931). On periodic leaf-change and flowering of trees in Singapore. *Gdns' Bul. Straits Settl.* **5**, 173–206.

Janzen, D. H. (1967). Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution, Lancaster, Pa.* **21**, 620–37.

Keller, C. O. (1946). An ecological study of the Klein Woods, Jennings County, Indiana. *Butler Univ. bot. Stud.* **8**, 64–81.

Lawton, J. R. S. & Akpan, E. E. J. (1968). Periodicity in *Plumeria*. *Nature, Lond.* **218**, 384–6.

List, R. J. (1951). Smithsonian meteorological tables, 6th edn. *Smithson. misc. Collns*, **114**.

Lojan, J. (1968). Tendencias del crecimiento de 23 especies forestales del tropico. *Turrialba*, **18**, 275–81.

Misra, R. (n.d.) *A comparative study of net primary productivity of dry deciduous forest and grassland at Varanasi, India.* Typescript, pp. 12.

Njoku, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. *J. Ecol.* **52**, 19–26.

Potzger, J. E., Friesner, R. C. & Keller, C. (1942). Phytosociology of the Cox Woods: a remnant of forest primeval in Orange County, Indiana. *Butler Univ. bot. Stud.* **5**, 190–221.

Servicio meteorologico Nacional de Costa Rica (1963). *Annuario Meteorologico.* San José.

Walter, H. (1964, 1968). *Die Vegetation der Erde in oeko-physiologischer Betrachtung.* 2 Vols. Fischer, Stuttgart.

Whitehead, D. R. (1969). Wind pollination in the angiosperms: evolutionary and environmental considerations. *Evolution, Lancaster, Pa.* **23,** 28–35.

(*Received* 11 *May* 1971)