



British Ecological Society

---

Water Stress and Tree Phenology in a Tropical Dry Forest in the Lowlands of Costa Rica

Author(s): Peter B. Reich and Rolf Borchert

Source: *Journal of Ecology*, Vol. 72, No. 1 (Mar., 1984), pp. 61-74

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/2260006>

Accessed: 16-07-2018 13:46 UTC

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



JSTOR

*British Ecological Society* is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Ecology*

## WATER STRESS AND TREE PHENOLOGY IN A TROPICAL DRY FOREST IN THE LOWLANDS OF COSTA RICA

PETER B. REICH\* AND ROLF BORCHERT

*Department of Physiology and Cell Biology, University of Kansas, Lawrence, Kansas 66045, U.S.A.*

### SUMMARY

(1) Phenology and seasonal variations in water stress, as indicated by variations in girth, were monitored for 1 yr in numerous trees of twelve species, growing at dry and moist sites in a tropical lowland deciduous forest in Guanacaste, Costa Rica.

(2) At dry sites, trees experienced water stress and shed their leaves early in the dry season. In most species, rehydration, followed by bud break, took place only after heavy rainfalls.

(3) In some species, leaf shedding was followed by rehydration and bud break during continuing drought.

(4) During shoot extension, which rarely lasted longer than a few weeks, trees experienced water stress in spite of growing in wet soils.

(5) At wet sites, trees experienced little or no apparent water stress; they remained evergreen or rapidly exchanged leaves during the dry season.

(6) In general, the timing of leaf fall and bud break and, in many species, anthesis was determined to a large extent by changes in tree water status. These phenomena, in turn, were a function of the interaction between the water status of the environment and the structural and functional state of the tree. At times the functional state of the tree would counteract the environmental influences; trees with growing shoots experienced temporary water deficits during the wet season, and bare trees rehydrated during drought.

(7) The seasonal pattern of tree development had a high correlation with seasonal variation in tree water status, but only indirectly with environmental water availability. No evidence was found for the control of tree development by seasonal variation in photoperiod or temperature.

### INTRODUCTION

It has long been recognized that seasonal changes in the physiognomy of tropical forests are caused primarily by seasonal variation in rainfall (Schimper 1898), which in conjunction with soil moisture availability is the principal determinant of tree water status (Longman & Jenik 1974; Doley 1981). Thus, the seasonal variation in water availability should determine the seasonal development in tropical trees, just as the phenology of deciduous temperate trees is determined primarily by seasonal changes in temperature and photoperiod. Also, tropical tree development should be arrested during drought and proceed actively during periods of adequate rainfall. In many tropical deciduous forests, the major phenological events conform to these expectations (Frankie, Baker & Opler 1974, and references cited therein); usually, leaves are shed during the early dry season and new shoots emerge after the onset of the wet season. However, many developmental events do not correlate with seasonal precipitation patterns: (i) tropical trees frequently

Present address: Boyce Thompson Institute, Cornell University, Ithaca, New York 14853, U.S.A.

flower during the early dry season after leaf fall; (ii) bud break may occur during the dry season; (iii) usually, shoot elongation and leaf expansion are limited to a few weeks during the early wet season and cease under conditions apparently favourable for growth; and (iv) trunks often shrink temporarily during the wet season and expand during continuing drought (Daubenmire 1972; Borchert 1980; Reich & Borchert 1982). Thus, several authors have warned against the attempt to infer causal relations from correlations between tree development and rainfall. Instead, variations in temperature and photoperiod were considered to trigger various phases of tree development (Njoku 1963; Frankie *et al.* 1974; Longman & Jenik 1974).

In view of the well established positive correlation between seasonal changes in girth and xylem water potential (Alvim 1975; Hinckley, Lassoie & Running 1978; Reich & Borchert 1982), Daubenmire's (1972) records of seasonal variation in girth of tropical trees imply that changes in tree water status are not always correlated with, and hence not directly caused by variations in water availability. Detailed analyses of the interrelations between environmental conditions, water status and phenology of the tropical deciduous trees *Erythrina poeppigiana* (Borchert 1980) and *Tabebuia neochrysantha* (Reich & Borchert 1982) showed that their water balance depended on soil moisture availability, atmospheric evaporative demand, and the transpirational capacity of the tree. Changes such as leaf fall and leaf expansion were found to cause changes in tree water status which, in turn, triggered the seemingly anomalous developmental events described above.

This paper is based on new records of seasonal changes in water status and on phenology of trees of numerous species in a tropical deciduous forest, and extends the earlier work of Borchert (1980) and Reich & Borchert (1982).

### SPECIES, SITES AND METHODS

Mature trees of twelve species were examined (Table 1). Except for the genus *Tabebuia*, after first mention, experimental tree species will be referred to by their generic name only.

TABLE 1. Numbers of trees of twelve species studied during 1978 at various sites at La Pacifica (Guanacaste, Costa Rica) and Alajuela (Costa Rica).

Site*	A	B	C	D	E	Total number	dbh $\pm$ 1 S.E. (cm)
Tree species	Number of trees at each						
<i>Albizzia caribaea</i> (Urban) Britt. and Rose				1		1	51.9
<i>Astronium graveolens</i> Jacq.			2			2	33.6 $\pm$ 1.6
<i>Bursera simaruba</i> (L.) Sarg.	2		9	3	3	17	35.6 $\pm$ 2.9
<i>Cochlospermum vitifolium</i> (Willd.) Speng.		2	9		1	12	27.8 $\pm$ 1.7
<i>Cordia alliodora</i> (R. & P.) Cham.			9			9	28.6 $\pm$ 2.0
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.		5	2	1	1	9	66.7 $\pm$ 3.4
<i>Guazuma tomentosa</i> H., B. and K.	10		1			11	22.9 $\pm$ 0.7
<i>Licania arborea</i> Seem.			1			1	41.4
<i>Lonchocarpus minimiflorus</i> Donn-Smith			4			4	23.8 $\pm$ 1.4
<i>Lysiloma seemannii</i> Britt. and Rose			2			2	31.3 $\pm$ 0.3
<i>Spondias purpurea</i> L.	1		5	6	4	16	24.4 $\pm$ 1.3
<i>Tabebuia rosea</i> (Bertol.) DC.	1			5	2	8	29.6 $\pm$ 1.8

\* Sites and (in parentheses) moisture classes:

A, riparian forest, Corobici River (wet to intermediate), La Pacifica.

B, irrigated woodland, near Corobici River (wet to intermediate), La Pacifica.

C, upland dry forest, near Corobici River (dry), La Pacifica.

D, upland dry forest, near Tenorio River (dry), La Pacifica.

E, Estación Experimental Fabio Baudrit (dry), Alajuela.

The range of these species extends from Mexico to northern South America and from tropical dry to moist forests (Hueck 1966; Hueck & Seibert 1972; Holdridge & Poveda 1975). Dry sites were at least 50 m away from and 10 m above a river or an irrigation canal; wet sites were within 10 m of water, and were usually on the bank of a river or irrigation canal; and intermediate sites were 20–50 m away from and 3–6 m above a water course.

Most observations were made at Hacienda La Pacifica, Guanacaste Province, Costa Rica, hereafter called La Pacifica (10°N, 85°W; altitude 45 m), which is described in Daubenmire (1972) and Reich & Borchert (1982). La Pacifica is considered to be in the 'tropical dry forest, moist province transition' (Holdridge 1967), with a climate typical of the Pacific watershed of Costa Rica (mean monthly temperature 28 °C, annual variation of the monthly mean approximately 1 °C; (Daubenmire 1972; Frankie *et al.* 1974). The dry season usually begins in late November and extends until early May. The remainder of the year is rainy and humid. A few individuals of five tree species (Table 1) were also observed at Alajuela, Costa Rica (10°N, 84°W; altitude 900 m), where temperature and atmospheric evaporative demand are slightly lower and the dry season is less severe than at La Pacifica (Borchert 1980).

From February 1978 to February 1979, observations of tree phenology and measurements of girth were made at weekly intervals, except for July to November 1978, when intervals between observations were 14 or 21 days. The variation in gbh of 10–15 m high trees was measured with aluminium dendrometer bands (Liming 1957), tested as described by Reich & Borchert (1982). Changes in girth and tree water status are highly correlated (Alvim 1975; Hinckley *et al.* 1978; Reich & Borchert 1982). Stem shrinkage during consecutive days indicates a decline in pre-dawn water potential; rapid, rain-induced stem expansion after a period of stem shrinkage reflects rehydration; and cambial activity is indicated by a gradual, long-term increase in the girth of fully hydrated trees. Patterns of seasonal girth change were very similar for trees of the same species growing at the same site, as indicated in some cases in Figs 1 and 2. Thus, the results in Figs 1 and 2 are representative of all experimental trees listed in Table 1.

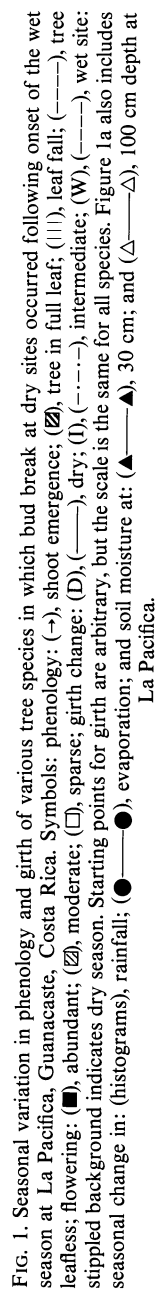
Soil moisture was determined with gypsum electrical resistance blocks calibrated as described by Reich & Borchert (1982), and data on Piche evaporation for the weather station Liberia (40 km NW of La Pacifica) were obtained from the Servicio Meteorológica Nacional de Costa Rica.

## RESULTS

### *Phenology and water status in Bursera and Spondias*

To illustrate the interpretation of records of seasonal variation in girth, observations with *Bursera* and *Spondias* will be discussed in detail (Fig. 1a, b).

At dry forest sites, soil moisture began to decline soon after the cessation of the wet season (Fig. 1a). Stems began to shrink, indicating a declining water potential, and leaves were shed. In *Bursera* (Fig. 1b), but not in *Spondias* (Fig. 1a), decreased transpiration after leaf fall permitted a temporary girth increase in December. In other species, such temporary rehydration during the dry season may be followed by flowering (e.g. *Cochlospermum*, Fig. 1c; *Tabebuia neochrysantha* (Reich & Borchert 1982)) or bud break (*Erythrina* (Borchert 1980)). Stem shrinkage continued in leafless trees until April. The first heavy rain caused rapid girth growth, the magnitude of which was a measure of preceding dry season shrinkage. Light rainfall caused only partial, temporary rehydration



(small peak in April, Fig. 1b) as in *Tabebuia neochrysantha* (Reich & Borchert 1982). Complete rehydration was rapidly followed by flowering in *Bursera* and by bud break in both species. During leaf expansion, stems temporarily ceased to expand or shrunk (Fig. 1a, b); (Daubenmire 1972; Lieberman 1982; Reich & Borchert 1982). Apparently, water loss by immature leaves exceeded the absorbing capacity of the root system. Stem shrinkage during the following months suggests that even during the wet season the water supply at dry sites may be suboptimal, particularly during the July–August dry period (Fig. 1a).

At wet sites, leaf fall in *Bursera*, but not in *Spondias*, was 6 weeks later than at dry sites. Stem shrinkage was minimal, and both species flushed late in the dry season during continued drought (Fig. 1a, b). These observations with *Bursera* and *Spondias* closely parallel observations made with *Tabebuia neochrysantha* (Reich & Borchert 1982).

#### *Phenology and water status at dry sites*

The basic pattern discussed above for *Bursera* and *Spondias* was observed in a group of tree species possessing either mesomorphic leaves and thin, smooth bark (*Bursera*, *Cochlospermum*, *Spondias*; Fig. 1a–c) or more xeromorphic leaves and thick bark (*Cordia*, *Gauzuma*, *Lonchocarpus*, *Lysiloma*, *Tabebuia rosea*; Fig. 1d–h). Generally, the more xeromorphic species shed leaves about 1 or 2 months later than the more mesomorphic ones. In contrast to all other species, bud break occurred several weeks after rehydration in *Lonchocarpus* and *Lysiloma* (Fig. 1f, g).

At the same dry sites (Table 1), the effects of water stress were less apparent in *Albizzia*, *Astronium*, *Enterolobium* and *Licania* (Fig. 2). These trees shrunk only moderately during the early dry season, their stems expanded little prior to bud break (except of *Licania*), and their leafless period was much shorter. *Enterolobium* shed its leaves in January and produced new shoots in March before any rain had fallen (Fig. 2a); *Albizzia* lost its leaves in February and bud break occurred immediately (Fig. 2b); *Astronium* increased in girth and underwent a rapid leaf exchange toward the end of the dry season (Fig. 2c); and *Licania* produced new leaves in April and May after losing only a few leaves (Fig. 2d). While leaves of *Astronium* and *Licania* are thick and sclerophyllous, *Albizzia* and *Enterolobium* possess more mesomorphic leaves and probably, like other Mimosaceae, a deep root system. Also, these individuals were very large in comparison with the other species studied (Table 1). This great size, which is typical for these species, suggests they have an extensive root system.

Temporal relations between flowering, vegetative growth and water stress were highly variable between species. *Albizzia*, *Enterolobium*, and *Lysiloma* flowered after the emergence of new shoots (Figs 1g, 2a, b). All other species flowered during the dry season, or during or after leaf fall. This implies that floral primordia had been laid down during the previous growing season and the buds had remained dormant for at least 6 months. Flowers opened during leaf fall in *Cordia* (Fig. 1d), and after leaf shedding and subsequent rehydration in *Cochlospermum* and *Tabebuia rosea* (Fig. 1c, h), in the middle of the dry season in *Guazuma* and *Spondias* (Fig. 1a, e), and after rehydration at the end of the dry season, immediately before shoot emergence, in *Bursera* (Fig. 1b).

#### *Phenology and water status at wet sites*

At wet sites, trees shrank only little and the leafless period was shorter than at dry sites. *Bursera*, *Cochlospermum* and *Spondias* retained their leaves slightly longer at wet than at dry sites and produced new leaves before the first rain (Fig. 1a–c). *Enterolobium* and

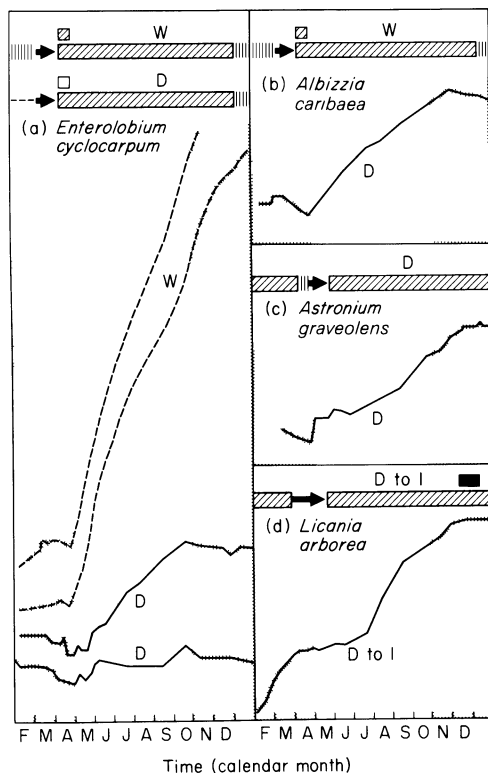


FIG. 2. Seasonal variation in phenology and girth in various tree species in which bud break at dry sites occurred during continued drought at La Pacifica, Guanacaste, Costa Rica. Other details as in Fig. 1.

*Guazuma* retained their leaves until March, then shed leaves and flushed in rapid sequence (Figs 1e, 2a).

In contrast to all other individuals of this species, a riparian *Tabebuia rosea* (Table 1, site A) exchanged leaves during the late wet season, then retained its foliage and increased its girth throughout the dry season, but never flowered (Fig. 1h). Absence of flowering was also observed in riparian *T. neochrysantha* at La Pacifica (Reich & Borchert 1982) and in other *T. rosea* trees which grew at wet sites in San José, Costa Rica, and whose seasonal development was several months out of phase with other trees of the species (Borchert 1982).

## DISCUSSION

### *Principal growth patterns*

The observed developmental patterns can be grouped in three main classes (Fig. 3):

- A, deciduous trees with synchronous bud break among individuals within a population;
- B, deciduous trees with asynchronous bud break among individuals within a population;
- and
- C, evergreen or leaf exchanging trees.

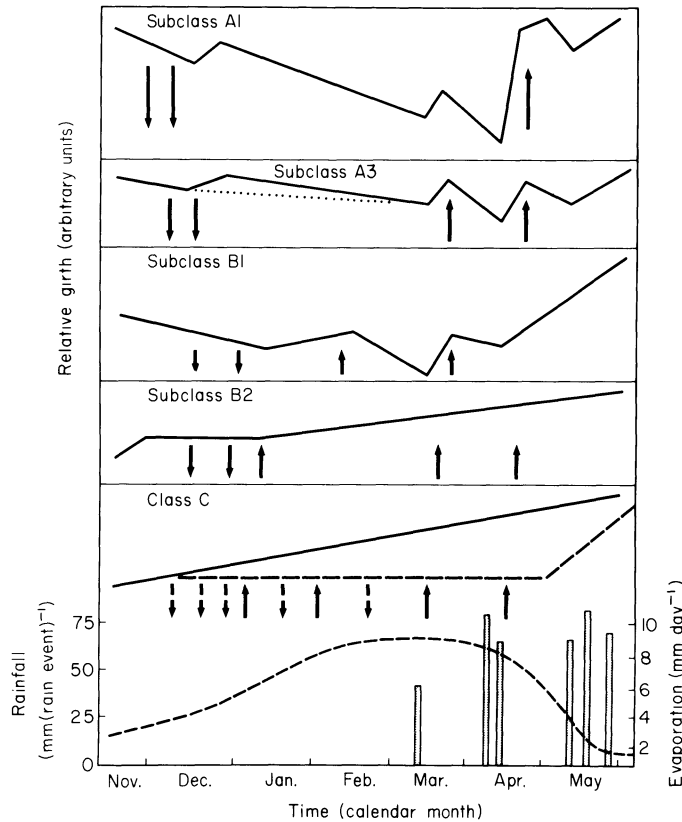


FIG. 3. Generalized seasonal patterns (classes A, B, C) of relations between seasonal variation in environmental factors (-----), Piche evaporation; histograms, rainfall; (—), relative changes in girth (arbitrary units) as indicators of tree water status (-----), alternative pattern within class, and tree development: leaf fall: (↓), complete; (↓), partial; (↑), shoot emergence during the dry and early wet season in Guanacaste, Costa Rica.

These classes represent a series of developmental patterns reflecting a decrease in the water stress of trees during the dry season, a decrease in the control of the timing of tree development by drought, and the resulting transition from a markedly deciduous to an evergreen growth habit. They are similar to those proposed by Koriba (1958) and Longman & Jenik (1974), but our definitions include the functional changes postulated to account for observed patterns. Subclasses (designated A1, A2, A3, B1, B2, B3, C1, C2) indicate a decrease in the degree of internal dehydration during the dry season (in part due to differences in moisture supply among habitats). Tree species from this and other studies (Daubenmire 1972; Reich & Borchert 1982) were assigned to these classes and also tentatively grouped according to soil moisture availability and the tree's capacity for water uptake or control of water loss (Table 2)—the main factors assumed to be responsible for the observed variation in phenology.

This classification and the implied relations between environmental water status, tree water status, and phenology should be considered as a working hypothesis only, for it is based on incomplete and often arbitrarily collected data obtained by different authors working in different years and using different methods and observation criteria. As a



function of site and rainfall distribution, trees within any species will experience various degrees of water stress and hence may display more than one of the patterns and thus appear under more than one subclass in Table 2.

*Deciduous trees with synchronous bud break*

**Subclass A1.** During the early dry season, the stems shrink markedly and the leaves are shed within 4 weeks of the last substantial rain. During leaf fall, the stems may expand

TABLE 2. Developmental patterns (classes A–C) observed at sites of increasing soil moisture availability (top to bottom) among tree species of various degrees of xeromorphy in the deciduous forest of Guanacaste, Costa Rica.

Class	Species	Family	Site*	References§
Low soil moisture				
Low xeromorphy†				
A1	<i>Bombacopsis quinata</i>	Bombacaceae	DF	D
	<i>Bursera simaruba</i>	Burseraceae	DF	Fig. 1b
	<i>Cochlospermum vitifolium</i>	Cochlospermaceae	DF	Fig. 1c
	<i>Chomelia spinosa</i>	Rubiaceae	S	D
	<i>Guettarda macropserma</i>	Rubiaceae	F	D
	<i>Luehea candida</i>	Tiliaceae	F	D
	<i>Sapranthus palanga</i>	Annonaceae	F	D
	<i>Spondias mombin</i>	Anacardiaceae	S	D
	<i>Spondias purpurea</i>	Anacardiaceae	DF	Fig. 1a
Intermediate xeromorphy†				
A2	<i>Cordia alliodora</i>	Boraginaceae	DF	Fig. 1d
	<i>Dalbergia hypoleuca</i>	Papilionaceae	S	D
	<i>Guazuma tomentosa</i>	Sterculiaceae	DF	Fig. 1e
	<i>Lonchocarpus minimiflorus</i>	Papilionaceae	DF	D, Fig. 1f
	<i>Lysiloma seemannii</i>	Mimosaceae	DF	D, Fig. 1g
	<i>Piscidia carthaginensis</i>	Papilionaceae	S	D
	<i>Tabebuia neochrysantha</i>	Bignoniaceae	S, DF	D, RB
	<i>Tabebuia rosea</i>	Bignoniaceae	DF	Fig. 1h
High xeromorphy†				
B1	<i>Enterolobium cyclocarpum</i>	Mimosaceae	DF	D, Fig. 2a
	<i>Pithecolobium saman</i>	Mimosaceae	DF	R
C1	<i>Albizzia caribaea</i>	Mimosaceae	DF	Fig. 2b
	<i>Astronium graveolens</i>	Anacardiaceae	DF	Fig. 2c
Intermediate soil moisture				
Intermediate xeromorphy†				
A3	<i>Chlorophora tinctoria</i>	Moraceae	S	D
	<i>Cordia stellifera</i>	Boraginaceae	S	D
	<i>Godmania aesculifolia</i>	Bignoniaceae	S	D
	<i>Pterocarpus hayesii</i>	Papilionaceae	S	D
	<i>Swietenia macrophylla</i>	Meliaceae	F	D
B1	<i>Platymiscium dimorphandrum</i>	Papilionaceae	S	D
	<i>Sterculia apetala</i>	Sterculiaceae	F	D
	<i>Tabebuia neochrysantha</i>	Bignoniaceae	IF	RB
High xeromorphy†				
C1	<i>Licania arborea</i>	Chrysobalanaceae	R, F	D, Fig. 2d
	<i>Machaereum biovulatum</i>	Papilionaceae	S	D
	<i>Manilkara spectabilis</i>	Sapotaceae	F	D
	<i>Tectona grandis</i>	Meliaceae	F	D
	<i>Trichilia colimana</i>	Meliaceae	F	D

\* Sites: DF, dry forest; F, forest; IF, irrigated forest; R, riparian; S, savanna.

† Low xeromorphy: mesomorphic leaves, shallow roots. High xeromorphy: xeromorphic leaves and/or deep root.

§ References: D, Daubenmire 1972; RB, Reich & Borchert 1982; R, P. B. Reich, unpublished.

TABLE 2.—continued

Class	Species	Family	Site*	References§
High soil moisture				
Low xeromorphy†				
A2	<i>Calycophyllum candidissimum</i>	Rubiaceae	R	D
	<i>Spondias mombin</i>	Anacardiaceae	R	D
Intermediate xeromorphy†				
B2	<i>Anacardium excelsum</i>	Anacardiaceae	R	D
	<i>Bursera simaruba</i>	Burseraceae	R	Fig. 1b
	<i>Ceiba pentandra</i>	Bombacaceae	R	D
	<i>Cochlospermum vitifolium</i>	Cochlospermaceae	IF	Fig. 1c
	<i>Enterolobium cyclocarpum</i>	Mimosaceae	IF	Fig. 2a
	<i>Guazuma tomentosa</i>	Sterculiaceae	R	D, Fig. 1e
	<i>Hymenaea courbaril</i>	Caesalpinaceae	R	D
	<i>Spondias purpurea</i>	Anacardiaceae	R	Fig. 1a
	<i>Tabebuia neochrysantha</i>	Bignoniaceae	R	RB
C2	<i>Coccoloba caracasana</i>	Polygonaceae	R	D
	<i>Inga spuria</i>	Mimosaceae	R	D
	<i>Sloanea terniflora</i>	Tiliaceae	R	D
	<i>Sterculia apetala</i>	Sterculiaceae	R	D
	<i>Tabebuia rosea</i>	Bignoniaceae	R	Fig. 1h

temporarily, but eventually the bare trees continue to shrink. Light rainfall causes partial and temporary girth increase and flowering in some species, but heavy rainfall is required for full stem expansion and subsequent bud break, which is synchronous in all trees at a given site (Fig. 3, A1).

*Subclass A2.* A similar pattern to subclass A1, except that during the early dry season stem shrinkage is moderate and leaves fall several weeks later.

*Subclass A3.* Leaves fall early in the dry season as in subclass A2. There is little or no stem shrinkage in leafless trees. The amount of rainfall needed for rehydration and subsequent bud break is lower than in subclass A2 (Fig. 3, A3).

Class A represents a growth pattern determined by severe seasonal drought and, as expected, it predominates in the lowland forests in Guanacaste. About 90% of the eighty tree species for which Frankie *et al.* (1974) gave complete phenological records display this pattern, including the species considered predominant in the dry forest at La Pacifica (Gentry 1976). The degree of water stress and the time of development, and therefore the subclasses of class A in Table 2, vary with soil moisture availability (*Bursera*, Fig. 1b; *Cochlospermum*, Fig. 1c; *Spondias*, Fig. 1a), the intensity and time of rainfall (compare phenological records of Daubenmire (1972) and Frankie *et al.* (1974) with Figs 1 and 2), and leaf structure. Thus, mesomorphic leaves of trees such as *Bursera*, *Cochlospermum* and *Spondias*, are consistently shed early in the dry season, while coriaceous and sclerophyllous leaves of trees like *Cordia*, *Tabebuia neochrysantha*, and others, are usually retained longer. The threshold of rainfall required for rehydration and bud break probably varies with the degree of prior dehydration of the soil and trees; Daubenmire's (1972) data indicate that rainfalls of 20–40 mm caused bud break in moderately, but not strongly, water-stressed trees (Fig. 3, A3; Table 2). Rainfall greater than 50–60 mm appears to trigger flushing in most trees (Liebermann 1982; Reich & Borchert 1982). If bud break induced by isolated rain showers is followed by a period of drought, the trees will again experience water stress, and their leaves will fall or remain partially expanded and will not complete their development until subsequent heavy rain has fallen (Coster 1923; Daubenmire 1972; Frankie *et al.* 1974). Similarly, in leafless *Tabebuia neochrysantha*,

moderate rainfall induced only flower opening, and bud break occurred weeks later after heavy rainfall. In contrast, isolated, heavy rainfalls were followed by flowering and shoot emergence in rapid sequence (Reich & Borchert 1982).

Characteristically, shoot elongation and leaf expansion cease early in the wet season and only rarely are followed by further flushes of shoot growth. This cessation of shoot growth under favourable environmental conditions, often discussed in the context of periodic shoot growth (Njoku 1963; Romberger 1963; Longman & Jenik 1974), must be the consequence of correlative inhibition (Borchert 1978). Stem shrinkage during flushing, as observed during the early wet season, indicates that during shoot growth the water balance of a tree tends to be negative even when the soils are wet. Whether this temporary water stress causes the arrest of shoot growth is not known.

Because of the short, synchronous period of leaf expansion in May–June, during the early dry season (December–January) all leaves are 8–9 months old. In *Cordia glabra* and *Tabebuia rosea* stomatal control in apparently healthy leaves of that age had been largely lost (Borchert 1979; P. B. Reich & R. Borchert, unpublished). If this is also true for trees of the deciduous lowland forest, it might help to explain the rapid increase in water stress and leaf shedding during the early dry season.

#### *Deciduous trees with asynchronous bud break*

**Class B.** The trees exhibit slight to moderate stem shrinkage during the early dry season. Leaf fall during the middle or late dry season is followed by girth increase and bud break during continuing drought. Bud break is independent of rainfall and hence asynchronous among the trees of a population. Later rain may cause additional flushes of shoot growth (Fig. 3, B1, B2).

During the early dry season, the increasing evaporative demand and, in non-riparian trees, the declining soil moisture, impose increasing water stress on trees of class B and accelerate senescence and the shedding of leaves, which at this time are 10–12 months old and probably control water loss poorly (see above). Leaf fall reduces water loss dramatically, and the water uptake is apparently sufficient to rehydrate bare trees and cause shoot emergence during continued drought. This phenomenon and the observed stem shrinkage during shoot growth (e.g. Figs. 1a, 2a) illustrate how significant changes in tree structure and function which affect water usage may cause changes in a tree's water status and trigger subsequent developmental events which do not correlate with the water status of the environment. The rates of leaf fall and rehydration in different trees vary with leaf structure, available soil moisture, depth of the root system, and other variables and, therefore, bud break is asynchronous within a population.

The sequence 'increasing stem shrinkage–leaf fall–girth increase–bud break' was also observed in *Cordia glabra* and *Erythrina poeppigiana* growing at an altitude of 1200 m under moderate evaporative demand in soils of high water storage capacity (Borchert 1980; R. Borchert, unpublished). Similarly, Huxley & van Eck (1974) found a high temporal correlation between leaf fall and subsequent bud break irrespective of variations in climate.

Class B development was observed among trees at riparian (subclass B2; Table 2) and intermediate to dry sites (subclass B1; Table 2). Site differences in available soil moisture are reflected in seasonal changes in water status and tree development. In riparian trees, leaf fall during the dry season is likely to reflect the acceleration of leaf senescence by increased daily water stress. As such trees will rehydrate at night, no long-term stem

shrinkage occurs and increasing daily water stress cannot be inferred from dendrometer records (Alvim 1975). New shoots form soon after leaf fall and for the remainder of the dry season, the leaves are retained and the trees increase in girth (fig. 3, B2). Growth in girth after leaf change indicates a positive water balance of riparian trees bearing young mature leaves.

The pattern of leaf change in riparian trees parallels that of trees in the tropical rain forest of La Selva (Costa Rica) and elsewhere, which often shed leaves and flush during periods of drought (Frankie *et al.* 1974; Longman & Jenik 1974). This suggests that such flushing may also be the result of drought-induced shedding of old leaves. For example, in a Brazilian rain forest, rapid leaf exchange in four tree species (*Erythrina glauca*, *Lecythis pisonis*, *Simaruba amara*, *Tabebuia* sp.) followed a period of moderate drought and slow or no trunk growth (Alvim & Alvim 1978).

Class B type development at intermediate and dry sites (Fig. 3, B1; Table 2) reflects limited soil moisture availability in several ways: stems shrink during early drought and during leaf expansion; rehydration and bud break are slower than in riparian trees; new leaves remain small (Borchert 1980); and the first heavy rainfall in the late dry season induces a second flush of larger leaves. How these trees can rehydrate and flush without rain at sites where other species remain bare until after the first rain needs to be studied. Trees of subclasses B1 and C1 at dry sites are mostly Mimosaceae. These are very large trees and, like other genera of this family (e.g. *Acacia*), might possess root systems which penetrate deep into the volcanic tuff underlying the forests in Guanacaste and, hence, can absorb residual moisture (Daubenmire 1972).

#### *Evergreen or leaf exchanging trees*

*Class C.* Throughout the dry season, these trees shed part of their foliage, may flush repeatedly, particularly after rains, and may grow in girth. A complete leaf exchange may occur during the wet season.

During the early dry season, trees of class C shed many, though not all, of their leaves and replace them in a major flush of shoot growth. Slight leaf fall continues throughout the dry season and additional flushes of shoot growth are triggered by later rainfall (Fig. 3, C). This pattern suggests that the effects of water stress on the time of leaf fall and shoot emergence are moderate. While daily water deficits are likely to occur, long-term water stress is manifest only in a temporary arrest of stem expansion. This evergreen habit was observed in several species at riparian sites (subclass C2; Table 2; Frankie *et al.* (1974)), but also at sites of low to intermediate soil moisture (subclass C1; Table 2). *Tectona grandis* shed leaves in November (Daubenmire 1972) and entered the dry season with a new complement of leaves, while *Licania* changed its strongly xeromorphic leaves in the early wet season (Fig. 3; Daubenmire 1972); both species are deciduous elsewhere (Coster 1923; Allen 1956). *Manilkara spectabilis* was the only evergreen tree whose trunk shrank during drought (Daubenmire 1972).

#### *Water stress and tree growth periodicity*

The observed correlations between the seasonal variation in tree water status and development need not be interpreted to mean that tree growth periodicity is caused by periodic changes in water status or climate. Rather, variation in water status might affect the relative timing of certain phases of the tree's endogenous growth periodicity and may entrain it to the prevailing climatic periodicity. Periodic shoot growth is an inherent

characteristic of trees as perennial, woody plants (Romberger 1963), in which many organs have life-spans much shorter than the life-span of the whole organism and thus must be replaced periodically. Even under constant and optimum environmental conditions, a cohort of leaves formed during a flush of shoot growth will become senescent eventually and abscise. Under such conditions leaf abscission will trigger bud break (Holttum 1930; Wycherley 1973; Huxley & van Eck 1974; Borchert 1980). Also, a full complement of old leaves has been often observed to inhibit bud break (Romberger 1963; Huxley & van Eck 1974).

The duration of growth cycles depends on the longevity of the leaves, which in tropical trees ranges from less than 6 months to about 24 months (Koelmeyer 1959; Longman & Jenik 1974). In general, the life-span of delicate, mesomorphic leaves is shorter than that of xeromorphic leaves. For example, in San José (Costa Rica), *Erythrina poeppigiana*, which possesses mesomorphic leaves, changes leaves twice a year (Borchert 1980), while *Cordia glabra*, *Tabebuia rosea* and other species do so only once each year (Fournier 1969, 1976; Borchert 1982). Such differences in the species-specific longevity of leaves probably account for a good deal of the differences in the time of leaf fall.

Tree water stress accelerates leaf senescence and hence leaf shedding. At moist sites, leaf fall triggers rapid bud break, which thus—paradoxically—occurs earlier in water-stressed than in non-stressed trees. At dry sites, bud break is delayed until after the first rainfall (Fig. 3). Depending on the degree of seasonal drought, the development within tropical tree species may thus range from an evergreen to a deciduous pattern (Coster 1923; Longman & Jenik 1974). For example, along an altitudinal gradient of increasing water stress, *Erythrina poeppigiana* changed from an evergreen to a deciduous habit, and at sites where large trees were deciduous the small trees remained evergreen (Borchert 1980). Similarly, several tree species (*Bursera*, *Cochlospermum*, *Enterolobium*, *Spondias*, *Tabebuia neochrysantha*, and *T. rosea*) growing at dry sites at an altitude of 900 m (Alajuela, Costa Rica; Table 1), where the evaporative demand during the dry season is markedly lower than at La Pacifica, shrank and shed their leaves several weeks later than at La Pacifica. *Tabebuia neochrysantha* displayed class A behaviour at dry sites, but class B behaviour at wet sites (Reich & Borchert 1982), and at a riparian site a tree of the deciduous *T. rosea* remained green throughout the dry season after having changed its leaves in the late wet season (Fig. 1h). Less dramatic, but marked effects of soil moisture availability on the phenology and seasonal tree water status are manifest in Figs 1 and 2. Experimental work with young trees of cacao (Alvim & Alvim 1978) provides excellent examples for these interactions and supports the proposed concepts.

### Water stress and flowering

In broadleaved trees, flowers may open either during or shortly after seasonal shoot growth or, as in the majority of deciduous tropical and temperate trees, after a period of flower bud dormancy, when trees are leafless. In tropical deciduous forests, flowering occurs commonly during the dry season (Janzen 1967; Frankie *et al.* 1974). Available evidence suggests that, like bud break, flower opening is triggered by leaf fall and the subsequent rehydration of previously water-stressed trees. For example, in four species of a tropical wet forest in Brazil (*Erythrina glauca*, *Lecythis pisonis*, *Simaruba amara*, *Tabebuia* sp.), flowers opened immediately after drought-induced leaf fall (Alvim & Alvim 1978)—a pattern identical with that of closely related species of *Erythrina* and *Tabebuia* growing at moist sites in Costa Rica (Fournier 1969; Reich & Borchert 1982; Borchert 1983). In deciduous trees, anthesis can be induced by the temporary rehydration of trees after leaf

fall (*Cochlospermum*, Fig. 3; *Tabebuia neochrysantha* (Reich & Borchert 1982); class B), by isolated rainfall during the dry season (Opler, Frankie & Baker 1976; Reich & Borchert 1982; class A), or by the onset of the wet season (*Bursera*, Fig. 2).

### *Bud dormancy*

In several tropical species, the rehydration of leafless trees does not always induce bud break; the trees are truly dormant during certain periods: (i) in *Lonchocarpus* and *Lysiloma* the buds opened about 4 weeks after the onset of heavy rain (Fig. 1f, g; Frankie *et al.* 1974); (ii) at wet sites, *Bursera*, *Cochlospermum*, and *Spondias* remained leafless for several months (Fig. 1a–c), (iii) in areas without a pronounced dry season, trees of the genera *Bombax*, *Bombacopsis*, *Cedrela*, *Cordia*, and others remain leafless for several months (Lojan 1967; Longman & Jenik 1974). *Cordia* stands bare for 2–4 months both in Turrialba and La Selva (Costa Rica) and the duration of the dormant period within the same population varies by at least 2 months (Lojan 1967; R. Borchert, unpublished). In teak and other species whose development is mainly determined by water status, bud break in detached, leafless twigs could be induced at any time by standing them in water, but branches of *Bombax* and other temporarily dormant species would flush at certain times only (Coster 1923; Njoku 1963).

### *Induction of bud break by variation in temperature or photoperiod*

In experimental work with seedlings and saplings of tropical trees, flushing of leafy trees was found to be inhibited by relatively low temperature and short photoperiod (Longman & Jenik 1974). Based on these and other studies, seasonal variation in temperature and photoperiod have been suggested as triggers of bud break in tropical trees (Daubenmire 1972; Frankie *et al.* 1974; Longman & Jenik 1974). However, the basis for such speculation appears weak for two reasons: (i) extrapolation of experimental results obtained with leafy tree seedlings to mature, leafless trees is questionable in view of the marked differences between the developmental patterns of young and old tropical trees (Borchert 1978); and (ii) the range of treatments required to obtain differences in tree development (temperatures of 23–30 °C, photoperiods of 9–17 h) was far greater than the natural variation of these factors in the tropics. In Costa Rica (latitude 10°N) photoperiod varies about 30 min during the year, and in southern Venezuela (latitude 1–2°N), where many of the species listed in Table 2 occur (Hueck & Seibert 1972), seasonal variations in day-length and monthly mean temperature are virtually absent. In view of the strong effect of variations in tree water status on the timing of development in trees, it appears unlikely that minute variations in photoperiod or temperature affect significantly the development of trees coping with prolonged seasonal drought as in Costa Rica and Venezuela.

## ACKNOWLEDGMENTS

We are grateful to the Werner Hagnauer family for permission to work on their property and for hospitality and logistic support; to earlier researchers who marked and classified many trees at La Pacifica; and to the National Science Foundation for financial support.

## REFERENCES

- Allen, P. H. (1956). *The Rain Forests of Golfo Dulce*. University of Florida Press, Gainesville.  
 Alvim, P. de T. (1975). A new dendrometer for monitoring cambium activity and changes in the internal water status of plants. *Turrialba*, **25**, 445–447.

- Alvim, P. de T. & Alvim, R. (1978).** Relation of climate to growth periodicity in tropical trees. *Tropical Trees as Living Systems* (Ed. by P. B. Tomlinson & M. H. Zimmermann), pp. 445–464. Cambridge University Press, Cambridge.
- Borchert, R. (1978).** Feedback control and age-related changes of growth in seasonal and nonseasonal climates. *Tropical Trees as Living Systems* (Ed. by P. B. Tomlinson & M. H. Zimmermann), pp. 497–516. Cambridge University Press, Cambridge.
- Borchert, R. (1979).** Complete loss of stomatal functioning in aging leaves of tropical broadleaved trees. *Plant Physiology*, **63**, 60.
- Borchert, R. (1980).** Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O. F. Cook. *Ecology*, **61**, 1065–1074.
- Borchert, R. (1983).** Phenology and control of flowering in tropical trees. *Biotropica* (in press).
- Coster, C. (1923).** Lauberneuerung und andere periodische Lebensprozesse in dem trockenen Monsungebiet Ost-Javas. *Annales du Jardin botanique Buitenzorg*, **33**, 117–189.
- Daubenmire, R. (1972).** Phenology and other characteristics of tropical semi-deciduous forest in northeastern Costa Rica. *Journal of Ecology*, **60**, 147–170.
- Doley, D. (1981).** Tropical and subtropical forests and woodlands. *Water Deficits and Plant Growth*, Vol. VI (Ed. by T. T. Kozlowski), pp. 209–323. Academic Press, New York.
- Fournier, L. A. (1969).** Estudio preliminar sobre la floración en el Roble de Sabana, *Tabebuia pentaphylla* (L.) Hemsl. *Revista de Biología Tropical*, **15**, 259–267.
- Fournier, L. A. (1976).** Observaciones fenológicas en el bosque humedo de premontano de San Pedro Montes de Oca, Costa Rica. *Turrialba*, **26**, 54–59.
- Frankie, G. W., Baker, H. G. & Opler, P. A. (1974).** Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881–919.
- Gentry, A. H. (1976).** Bignoniaceae of southern Central America: distribution and ecological specificity. *Biotropica*, **8**, 117–131.
- Hinckley, T. M., Lassoie, J. P. & Running, S. W. (1978).** Temporal and spatial variations in the water status of forest trees. *Forest Science Monograph*, **20**.
- Holdridge, L. R. (1967).** *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica.
- Holdridge, L. R. & Poveda, L. J. (1975).** *Arboles de Costa Rica*. Tropical Science Center, San José, Costa Rica.
- Holttum, R. E. (1930).** On periodic leaf change and flowering of trees in Singapore. *Gardens' Bulletin, Singapore*, **5**, 173–206.
- Hueck, K. (1966).** *Die Wälder Südamerikas*. Fischer, Stuttgart.
- Hueck, K. & Seibert, P. (1972).** *Vegetationskarte von Südamerika*. Fischer, Stuttgart.
- Huxley, P. A. & van Eck, W. A. (1974).** Seasonal changes in growth and development of some woody perennials near Kampala, Uganda. *Journal of Ecology*, **62**, 579–592.
- Janzen, D. H. (1967).** Synchronization of sexual reproduction of trees within the dry season of Central America. *Evolution*, **21**, 620–637.
- Koelmeyer, K. O. (1959).** The periodicity of leaf change and flowering in the principal forest communities of Ceylon. *Ceylon Forester*, **4**, 310–364.
- Koriba, K. (1958).** On the periodicity of tree growth in the tropics. *Gardens' Bulletin, Singapore*, **17**, 11–81.
- Lieberman, D. (1982).** Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology*, **70**, 791–806.
- Liming, F. G. (1957).** Homemade dendrometers. *Journal of Forestry*, **55**, 575–577.
- Lojan, L. (1967).** Periodicidad del clima y del crecimiento de especies forestales en Turrialba, Costa Rica. *Turrialba*, **17**, 71–83.
- Longman, K. A. & Jenik, J. (1974).** *Tropical Forest and its Environment*. Longman, London.
- Njoku, E. (1963).** Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. *Journal of Ecology*, **51**, 617–624.
- Opler, P. A., Frankie, G. W. & Baker, H. G. (1976).** Rainfall as a factor of the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography*, **3**, 231–236.
- Reich, P. B. & Borchert, R. (1982).** Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology*, **63**, 294–299.
- Romberger, J. A. (1963).** *Meristems, Growth, and Development in Woody Plants*. U.S. Department of Agriculture Technical Bulletin No. 1293.
- Schimper, A. F. W. (1898).** *Pflanzengeographie auf Physiologischer Grundlage*. Fischer, Jena.
- Wycheley, P. R. (1973).** The phenology of plants in the humid tropics. *Micronesica*, **9**, 75–96.

(Received 23 February 1983)