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# PHENOLOGY AND ECOPHYSIOLOGY OF THE TROPICAL TREE, *TABEBUIA NEOCHRYSANTHA* (BIGNONIACEAE)[1]

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*Abstract.* Phenology and seasonal variations in water stress, as reflected in variations in stem circumference, were monitored throughout 1978 in numerous *Tabebuia neochrysantha* growing at several dry and wet sites in a lowland deciduous forest in Guanacaste, Costa Rica. The rate of leaf fall during the early dry season was strongly correlated with the decline in soil moisture and increasing water stress of the trees. Without exception, recovery from water strees was required for flowering and shoot emergence. At dry sites rehydration occurred only after isolated rain showers or irrigation; at wet sites it took place during continued drought, probably as a consequence of the decrease in transpiration during leaf fall. Flowering has been observed to occur at any time between the beginning (December) and end (May) of the dry season. Differences in the timing and intensity of flowering as well as in the timing of leaf fall and shoot emergence can be accounted for by site-dependent differences in the rates of desiccation and rehydration of trees in conjunction with year-to-year variation in the timing and intensity of rainfall. No evidence for the control of seasonal development by other environmental factors, such as variations in temperature of photoperiod, was obtained.

*Key words: phenology of tropical trees;* Tabebuia neochrysantha; *tropical deciduous forest; water stress.*

## INTRODUCTION

The main climatic difference between tropical deciduous and evergreen forests consists in length and severity of the dry season. Throughout the tropics, but especially in deciduous forests, seasonal fluctuations in precipitation are great in comparison with variations in temperature. The phenology of various tropical deciduous trees has been studied in Costa Rica (Daubenmire 1972, Frankie et al. 1974, Fournier 1976) and in Africa (Njoku 1963, Hopkins 1970), but the ecophysiology of tropical deciduous trees is all but unknown.

In many tropical forests increased leaf fall has been correlated with the onset of the dry season, but the relationships between seasonal climatic changes and other phases of tree phenology are not well understood. Most trees in tropical deciduous forests flower during the dry season, and leaf flushing in many deciduous species occurs prior to the onset of the rainy season (Rawitscher 1948, Webb 1959, Boaler 1966, Daubenmire 1972, Longman and Jenik 1974). While slight changes in temperature (Walter 1971, Longman and Jenik 1974) or photoperiod (Njoku 1964, Daubenmire 1972, Frankie et al. 1974) have been suggested as possible triggers of bud break, the key question concerning the tree's capacity for flowering, bud break, and leaf growth under continued drought has never been stated, much less answered. How can trees that suffered drought-induced leaf abscission rehydrate and undergo anthesis, shoot growth, and leaf expansion, before the onset of rains?

Correlations between phenology and seasonal variations in stem diameter of trees observed in a tropical deciduous forest (Daubenmire 1972) might provide an answer to this question. Daubenmire found that as the dry season proceeded and drought became more pronounced, trees eventually shed their leaves. Leaf fall was accompanied by marked stem shrinkage, indicating a declining xylem pressure potential. Soon after the completion of leaf fall stem diameters increased rapidly, reflecting rehydration of the trees, and bud break occurred. As these changes happened during apparently continued drought, we interpreted them as follows: during early drought transpirational water loss exceeds water absorption by the root system. The tree water potential declines and causes leaf senescence and subsequent leaf shedding. After the reduction in transpirational water loss, slow absorption of residual soil moisture suffices to increase tree water potential and permit bud break, as was found by Borchert (1980).

To test this hypothesis, phenology and seasonal changes in stem circumference, as a measure of water status, were monitored for 1 yr in numerous *Tabebuia neochrysantha* trees growing in a tropical lowland deciduous forest in Costa Rica.

## MATERIALS, STUDY SITES, AND METHODS

### *Study species*

*Tabebuia neochrysantha* A. Gentry (=*Tabebuia ochracea* ssp. *neochrysantha* A. Gentry, Bignoniaceae) is a tree up to 25 m tall and 50 cm dbh with

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TABLE 1. Description and classification of study sites at La Pacifica, Cañas (Guanacaste).

| Site | Location | Moisture class | No. trees |
|---|---|---|---|
| A | Gallery forest along Corobici River | wet | 4 |
| B | Forest near Corobici River | intermed. | 4 |
| C | Dry forest 25 m above Corobici River | dry | 9 |
| D | Dry forest 75 m above Corobici River | dry | 6 |
| E | Dry forest near Tenorio river | dry | 5 |
| F | Clearing near restaurant "La Pacifica" | intermed. | 4 |
| G | Pasture in Hacienda Corobici, near La Pacifica | dry | 3 |

furrowed bark, palmate five-foliate leaves, large conspicuous yellow flowers, and pod-like fruits of up to 30 cm length. It occurs from Honduras and El Salvador to Venezuela and Trinidad and ranges from tropical dry forests to the drier parts of tropical moist forests (Gentry 1974*a*). Along with *Cochlospermum vitifolium, Spondias purpurea* and *Lonchocarpus minimiflorus,* it has been identified as one of the dominant trees in the upland dry forest at Hacienda La Pacifica, Guanacaste Province, Costa Rica (Gentry 1976).

Like the closely related *Tabebuia rosea, Tabebuia neochrysantha* is a tree of determinate shoot growth and sympodial branching, similar to the temperate *Rhus typhina* (Hallé et al. 1978, R. Borchert, *personal observations*). Unless growing at riparian sites, the tree sheds its leaves during the dry season. Flushes of shoot growth are initiated by the simultaneous outgrowth of two opposite lateral buds subtending the terminal inflorescence. After forming relatively few leaves, the apical meristem ceases to grow and forms flower primordia. Most branches on mature trees probably flush only once a year, and active shoot growth is limited to 1 or 2 mo during the early rainy season. As in many temperate and tropical trees, flowers open many months after their inception at the apical meristem and only after leaves have become senescent or have abscised, yet before the emergence of new shoots.

### *Study area*

Most of the data were collected at Hacienda La Pacifica, located 4.5 km northwest of Cañas, at 45 m elevation (latitude 10°28′N, longitude 85°09′W). La Pacifica consists mostly of low, rolling hills between the Corobici and Tenorio Rivers and the Pan-American Highway. In the life zone classification system of Holdridge, La Pacifica is considered to be in the "tropical dry forest, moist province transition" (Tosi 1969). Although the natural vegetation of the area is seasonally dry deciduous forest, much of the land has been converted to pasture.

Thirty-five *T. neochrysantha* trees at seven locations were studied in detail (Table 1). Dry, intermediate, and wet sites were defined by distance from either a river or an irrigation source. Dry sites were always at least 50 m from, and 25 m above, any water source. Wet and intermediate sites were, respectively, within 10 m of, or further than 20 m from, water.

### *Climate*

La Pacifica has seasonal weather typical of the Pacific watershed of Costa Rica. Mean annual temperature is 28°C and variation of the mean from month to month is about 1° (Daubenmire 1972, Frankie et al. 1974). A long dry season generally begins in late November and extends until early May. The rest of the year is rainy and humid, and is often divided into two wet periods by a drier period in July–August. Mean annual precipitation is about 1700 mm, but both the amount and timing of annual rainfall vary widely from year to year. Since 1965 annual rainfall has ranged from 947 to 2233 mm, and the beginning and end of the rainy season have varied by as much as 2 mo (Data obtained from Instituto Nacional de Meteorología, San José, Costa Rica).

### *Irrigation experiment*

In early April 1978 four leafless *T. neochrysantha* trees growing on nearly level terrain in a dry forest (site C of Table 1) were sequentially irrigated at time intervals of 3 d. Each tree was watered for 12 consecutive h with a hose using water pumped from the Corobici River.

### *Measurement techniques*

Changes in stem circumference were measured (±0.13 mm) with aluminum dendrometer bands manufactured according to Liming (1957). Errors due to size fluctuations of aluminum with changes in temperature appeared to be minimal, because measured stem circumference of a dead tree did not change during a day with 10° air temperature fluctuation, nearly as great a daily or seasonal change as would normally occur. Xylem pressure potential was measured with a pressure chamber.

Diurnal and seasonal variations of stem circumference have been shown to be highly correlated with temporal fluctuations in water status of many tree species (Worrall 1966, Alvim 1975, Hinckley et al. 1978, Lassoie 1979) including *T. neochrysantha* (Fig. 1). Use of stem circumference as a measure of tree water status is thus well justified. The relatively small standard deviations of measurements of stem circumference (see Fig. 2 legend) indicate a high degree of synchrony with respect to variations in water stress experienced by trees at any given site. Observations

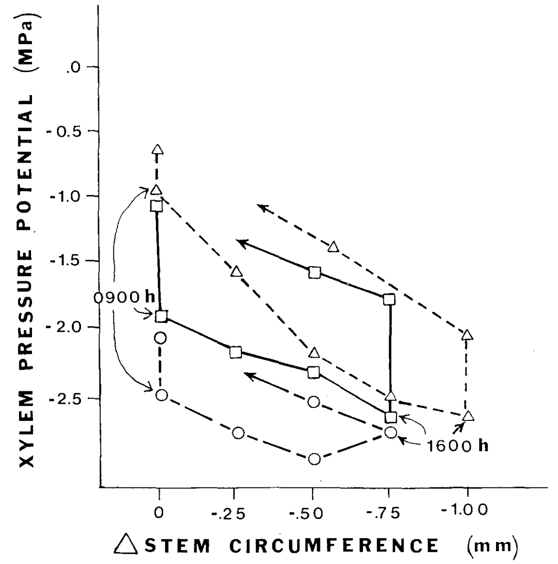

FIG. 1. Diurnal hysteresis loops relating stem circumference and xylem pressure potential of three *Tabebuia neochrysantha* trees in January 1979 (true solar time indicated).

of diurnal changes in *T. neochrysantha* showed that stem circumference was greatest approximately 2 h after sunrise and at a minimum in late afternoon. To minimize fluctuation due to diurnal changes, stem circumference was measured at 0800 at weekly intervals from 1 February until 1 July 1978, at approximately 21-d intervals between 1 July and 17 December 1978, and again at weekly intervals from 17 December 1978 until 1 February 1979.

A record of the phenological changes of studied trees was obtained by observing tree crowns with binoculars and noting the developmental status of leaves, flowers, and fruits in conjunction with measurements of stem circumference and estimates of relative leaf areas of trees.

Changes in soil moisture content were measured with porous gypsum blocks buried in October 1978 at three depths in nine locations at La Pacifica. The blocks were manufactured by the authors and calibrated by comparing changes in the measured resistance with changes in the gravimetric water content of the blocks during a drying cycle.

## RESULTS AND DISCUSSION

Phenology and seasonal changes in stem circumference of *T. neochrysantha,* as determined at wet, intermediate, and dry sites, are represented in Fig. 2 in relation to the relevant climatic variables. Additional observations are summarized in Table 2.

At dry forest sites, soil moisture declined rapidly during early drought, which led to increasing stem shrinkage and leaf shedding in seedlings and mature trees of *T. neochrysantha* (Fig. 2c). Even after leaves

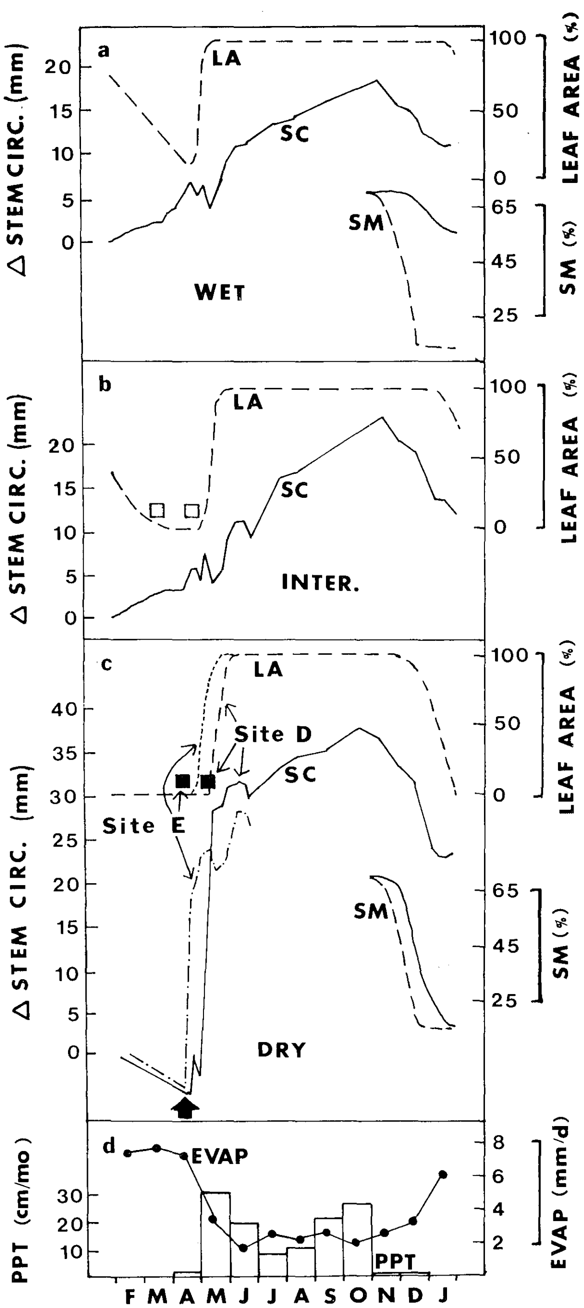

FIG. 2. Phenology and seasonal changes in stem circumference of *T. neochrysantha* exposed to various degrees of drought between February 1978 and January 1979. a—wet site (A of Table 1); b—intermediate site (B of Table 1); c—dry sites, D (———) and E (·—·—) of Table 1. On 19 April (heavy arrow in c) 20 mm rain fell at sites A, B, and D and 40 mm at site E. Relative leaf area of trees (LA), as percent of full canopy (– – – –). Changes in stem circumference (SC, ———) are means calculated from 4, 4, 5, and 6 trees at sites A, B, D, and E, respectively. Standard deviations were $<5$ mm in all groups. ■—full flowering (75% of flower buds opened), □—slight flowering (25% of buds opened). d—precipitation (histogram; PPT) per month and seasonal variation in Piche evaporation (EVAP). Changes in soil moisture (SM) measured at 30 (– – –) and 100 (———) cm depth during the early dry season are given for wet and dry sites as inserts in a and c.

TABLE 2. Phenological observations in *T. neochrysantha* at selected dry sites during the dry season 1978. Numbers at head of each column (2.1–2.5) are for identification.

| | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 |
|---|---|---|---|---|---|
| | >100 trees in Bagaces (20 km from Cañas) | 7 trees at edge of dry forest (near site E) | 4 trees in dry forest (Site C) | 4 trees near restaurant (Site F) | Young stem sprouts in dry pasture (Site G) |
| 15 Feb | all trees leafless | | | | in full foliage |
| | | | | | new flush of leaves formed |
| 1 Mar | rain showers | | | Continuous irrigation ↓ | |
| | many flowers open | | | | |
| 15 Mar | (shrubs/grass leafing out) | | | flowers ↓ | |
| | flowers fall | irrigation | | leaves emerge | |
| | | abundant flowers | | | |
| | | flowers fall | | | |
| 1 Apr | | | irrig. tree no. 1 ↓ flowers<br>irrig. tree no. 2 ↓ flowers<br>irrig. tree no. 3 ↓ flowers | | |
| 15 Apr | | 40 mm rain | | | |
| | | leaves emerge | | | |
| | heavy rainfall | | | | |
| 1 May | all trees are leafing out | | | already in leaf | |

had fallen, stem circumference continued to decline slowly throughout the drought period, indicating continuing dehydration of trees (Fig. 2c, February–March). At the same time, stem sprouts growing from the stumps of small, isolated trees in a pasture were able to flush and retain their leaves well into the dry season (Table 2:2.5), probably because of their large root/shoot ratio and the lack of competition for available soil moisture from roots of other trees (compare Borchert 1978).

Following drought, an increase in stem circumference at dry sites always required the provision of water in the form of rain or irrigation. The degree of rehydration and the tree's response varied strongly with the amount and timing of rainfall or irrigation. A single rainfall of 20 mm caused partial, and temporary, rehydration, but was insufficient to trigger the opening of flower buds (Fig. 2c, site D, late April). Rainfall or irrigation of intermediate intensity induced flowering not followed by shoot emergence (Table 2:2.1, 2.2, 2.3), and strong rainfalls or irrigation caused a substantial increase in stem circumference, flowering, and shoot emergence in rapid sequence (Fig. 2c, Table 2:2.4). Whenever the trees' development was arrested at an early stage of this sequence because of insufficient rehydration, they completed the remaining phases after additional rain had fallen (Fig. 2c, site D; Table 2:2.1–2.3).

The timing of shoot emergence after heavy rains depended upon topography and probably reflected the rate and degree of soil rehydration: flushing occurred first in bottomlands, then on mid-slopes, and last in trees growing on ridges. In each forest the understory layer of shrubs, herbs, and tree seedlings leafed out within a week after the rains and over a week before mature trees. Seedlings of *T. neochrysantha* were thus leafing out while mature trees were flowering.

At wet and intermediate sites, tree water potential clearly declined after the cessation of rains (Fig. 2a, b: stem shrinkage in December 1978 and January 1979). As trees slowly shed their leaves, water stress diminished in spite of the continued drought (Fig. 2a, b: slow increase in stem circumference in February to April 1978). While trees at intermediate sites flowered slightly twice (during drought after shedding all leaves and after the first rains; Fig. 2b), trees at wet sites retained some of their leaves and did not flower (Fig. 2a).

In agreement with the hypothesis proposed in the Introduction to explain Daubenmire's findings (1972), the observations at wet sites suggest the following. During the early dry season the gradual elimination of the transpirational surface by leaf shedding slowly reduces the water stress resulting from high evaporative demand. Only if all leaves are shed is water stress sufficiently reduced to permit partial anthesis under continued drought (Fig. 2b: March). Similarly, in the Central Valley of Costa Rica, an area experiencing only moderate drought as compared to Guanacaste, *T. neochrysantha* has been observed to flower in December, immediately following leaf fall (P. B. Reich, *personal observation*), and leaf shedding caused rehydration and shoot emergence in *Erythrina poeppigiana* under continued drought (Borchert 1980). The role of leaves and flowers in enhancing tree water stress is reflected in the distinct stem shrinkage experienced by trees at all sites after shoot emergence (Fig. 2a, b, c in May), and by trees at dry sites during flowering (Fig. 3), as well as in the temporary increase of stem circumference after leaf fall (Fig. 2c: January 1979), during continuing drought.

Most *T. neochrysantha* grew in girth throughout the rainy season, but variability between individuals was high. In general, the moister the site, the greater was radial growth during this period, suggesting that even during the rainy season water supply at dry sites limited growth at times. Soon after the cessation of rains, between late October and early November 1978, radial growth ended, first in trees at dry sites, followed by trees at the wetter sites (Fig. 2).

Year-to-year variation in the amount and timing of rainfall markedly affects the seasonal development of *T. neochrysantha*. Leaf fall occurred early after a "dry" rainy season (e.g., 1977) or one that ended early (e.g., 1978, Fig. 2). Conversely, the late leaf fall reported for 1970 by Daubenmire (1972) must have been the result of a long, wet, rainy season. Opler et al. (1976) observed a 1-mo difference in flowering of *T. neochrysantha* (early April 1972 vs. early May 1973) due to the timing of first rainfalls in two consecutive years.

Seasonal development in *T. neochrysantha* thus appears to be almost exclusively controlled by seasonal changes in tree water status. Variations in the timing of phenological events can be ascribed entirely to differences in the rates of desiccation during early drought and of later recovery from water stress. After having suffered drought-induced leaf shedding, trees will flower and leaf out whenever they have attained the water potential required for the occurrence of developmental processes involving cell expansion. Therefore, buds are never dormant during the dry season. Similarly, seeds of the tropical shrub *Hybanthus prunifolius* will germinate whenever exposed to the irregular rainshowers of the dry season in Panama (Augspurger 1979). As there is no physiologically feasible alternative explanation for the developmental patterns observed in *T. neochrysantha,* there is no reason to assume that the timing of its development might have evolved as a consequence of interaction with a biotic factor such as availability of pollinators or seed dispersal agents, as suggested by Janzen (1967), Frankie et al. (1974), Gentry (1974*b*), and Opler et al. (1976). Also, because flower buds in *T. neochrysantha* are terminal, they must be differentiated towards the end of a flush of shoot growth, i.e., during the early rainy season (May to July), a time of increasing photoperiod. Our observations of *T. neochrysantha* therefore do not support the postulated role of short photoperiods in flower induction of tropical trees (Opler et al. 1976).

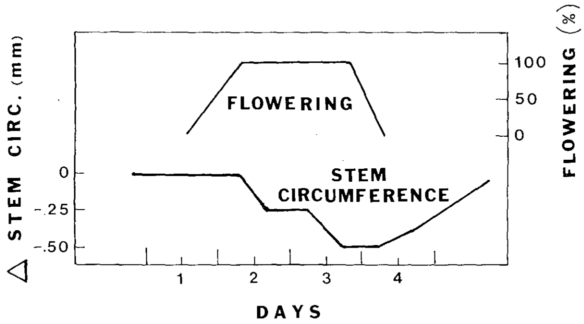

FIG. 3. Changes in stem circumference in a leafless tree as a consequence of flowering.

Our results suggest that in the absence of adequate measurements of precipitation or irrigation, the observed responses of *T. neochrysantha* and other deciduous forest species can be used as reliable bioindicators of changes in the relative water status of a site. The simultaneous flowering or flushing of many trees at a given site during the dry season will indicate an isolated rain shower, while developmental changes resulting from correlative rehydration after leaf shedding will be asynchronous in any given population of trees (Borchert 1980). We conclude that the simultaneous stem expansion and shoot emergence in many trees of the deciduous forest in Guanacaste, as observed by Daubenmire (1972) during the late dry season, must have been caused by isolated rain showers, and many reports in the literature concerning the leafing out of deciduous trees during the late dry season (see Introduction) can probably be ascribed to the same cause.

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