

## Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium collections.

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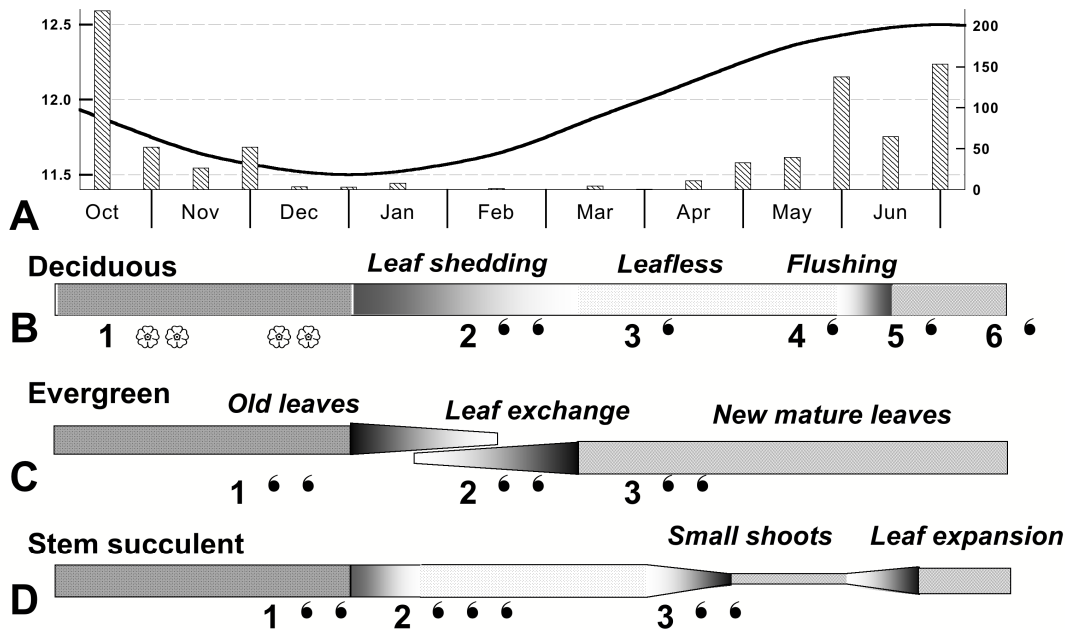
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**Summary.** During the late rainy season in October 1997 we observed, over a range of >100 km, the highly synchronous emergence of flower buds in several deciduous tree species of the semideciduous tropical forest in Guanacaste, Costa Rica. Synchronous flowering soon after the rapid decline in daylength around the September equinox and in the absence of any notable climatic cues suggested flower induction by declining photoperiod. Combining field observations and the analysis of flowering herbarium collections, we established for more than 25 tree species and a few herbs highly synchronous flowering periods with low inter-annual variation and latitudinal variation predicted for photoperiodic flower induction. We describe the morphogenetic changes at the shoot apex of three species during flower induction and the suppression and induction of flowering in several herbaceous species by experimental daylight extension. The combined observations provide strong, mainly indirect evidence for the photoperiodic induction of flowering in many tropical tree species. At low latitudes with annual variation in daylength of one hour, flower induction must be caused by a decline in photoperiod of 30 min or less. This is the first report of photoperiodic control of flowering in trees.

### Introduction

Like temperate trees, most tropical trees flower for relatively short periods at certain times of the year and during specific phases of seasonal vegetative development. Little is known about the environmental or endogenous controls of periodic flowering in temperate or tropical trees (Figure 1; Borchert 1983, 1992, 1996, 2000; Owens 1991, Dick 1995, Thomas and Vince-Prue 1997). In trees of seasonally dry tropical forests flowering may occur at several species-specific stages of seasonal vegetative development (Borchert 2000). Flowering is often closely associated with shoot growth: axillary flowers appear during flushing at the first nodes of expanding shoots (Figure 1: B5, C2, D3) or seasonal shoot growth ends with the transformation of the apical meristem into a terminal inflorescence (Figure 1: B6, C3). Shoot growth in deciduous, evergreen and stem succulent species occurs during different phases of the seasonal climatic cycle and is triggered by different cues (Borchert 2000, Borchert and Rivera 2000). The timing of periodic flowering associated with shoot growth therefore varies widely among species of different functional types (Figure 1, B June-July, C Feb-Apr, D Apr). In a few species of all functional types apical or lateral buds resume growth after several months of rest and form an inflorescence bearing flowers during the late rainy season (Figure 1, Oct-Dec, B1, C1, D1). In the above flowering patterns the induction of flowering meristems is likely to occur shortly before anthesis (Borchert 1983). In many deciduous species flower buds formed during the wet growing season remain arrested until bud expansion and anthesis are triggered during the dry season by rehydration resulting from leaf shedding (Figure 1: B2, D2; Borchert 1983, 1994a, 2000) or rainfall after prolonged drought (Figure 1: B 3,4; Opler et al. 1976, Reich and Borchert 1984, Bullock 1986, Borchert 1994a,b).



**Figure 1.** Variation in environmental factors (A; bars - rainfall/15 d; line - daylength) and seasonal development of deciduous, evergreen and stem succulent trees (B-D) as observed from October to July in the semideciduous forest of Guanacaste, Costa Rica (10°N). For each functional tree type vegetative phenology (*horizontal bars*) and observed species-specific flowering periods (*identified by numbers*) are given. For details see text.

Earlier analysis of flowering herbarium collections showed an abrupt onset of flowering in *Calycophyllum candidissimum*, *Cordia alliodora* and *Luehea speciosa* during Oct/Nov, a period without notable changes in climate or vegetative phenology (Figure 1; Figures 4, 5D, 6B in Borchert 1996). To identify the flowering cue, we monitored the transition from vegetative to reproductive development of these species during Oct/Dec 1997. In these and a few other species flower buds emerged within 2 weeks in all conspecific trees throughout the semideciduous forests of Guanacaste, Costa Rica (Figure 2; Table 1). Synchronous flower development in foliated trees soon after the rapid decline in daylength around the autumn equinox and in the absence of any notable biotic or climatic change suggested flower induction by declining photoperiod (Figure 1 A, B1). Conventional experimental methods used to analyze the role of photoperiod in the flower induction of herbs are impractical with trees flowering only when several m tall and several years old. We therefore established a set of partially redundant criteria as a screen to evaluate observed flowering patterns and to guide our search for additional tree species in which declining photoperiod might induce flowering. These criteria are introduced below to facilitate the evaluation of Methods and Results.

Observations in more than 25 tree species and a few herbaceous species, screened by the new criteria, provide powerful indirect evidence for the induction of flowering by a decline in photoperiod of less than 30 min. To our best knowledge, this is the first extensive documentation of photoperiodic control of flowering in trees (Owens 1991, Thomas and Vince-Prue 1997).

#### **Photoperiodic control of flowering in trees**

In many herbaceous plants and a few subtropical woody plants (*Bougainvillea*, *Euphorbia splendens* [poinsettia], *Hibiscus*) flowering can be induced or enhanced by experimental variation of photoperiod (Thomas and Vince-Prue 1997). Flower induction by declining photoperiod has

been shown experimentally for a single tree species, the West African *Hildegardia barteri*, in which a number of inflorescences expand in Oct-Dec from axillary buds near the apex of leafless shoots (Keay 1989). Flowering was completely suppressed in tree branches within 2 m of a street lamp (Hall et al. 1975) and saplings (60 -100 cm tall) flowered occasionally when exposed to 11.5 and 12 h photoperiods, but never under 12.5 h days (Njoku 1964). Vegetative development of temperate and tropical tree seedlings is known to be affected by exposure to different photoperiods (Njoku 1964, Stubblebine et al. 1978, Borchert and Rivera 2000). The following criteria constitute predictions that should be met by any tree species in which flowering is induced by declining photoperiod. None of these criteria alone will prove short-day induction of flowering, but confirmation of all or most criteria by several independent data sets constitutes powerful indirect evidence for such an induction.

*Criteria for flower induction in tropical trees by declining photoperiod*

**C1** - Flower development includes the formation of an inflorescence and flower buds shortly before anthesis (Figure 2). Visible, continuous development of an inflorescence or flower buds shortly before anthesis is essential for establishing the time of photoperiodic flower induction. Expansion of resting flower buds formed months before anthesis, as common among deciduous temperate and tropical tree species, precludes flower induction shortly before flowering.

**C2** - Flowering is synchronous among all conspecific trees in a landscape. Asynchronous flowering of conspecific trees growing at different microsites indicates control of phenology by site-dependent temporal variation in tree water status as opposed to photoperiodic control (Borchert 1994a, 2000).

**C3** - Flowering time does not vary from year to year. Lack of inter-annual variation in flowering time, and hence independence of inter-annual variation in climate, is a crucial characteristic of photoperiodic control.

**C4** - Trees flower every year. The regular occurrence of the photoperiodic cue should cause annual flowering.

**C5** - Flowering time varies predictably with latitude. With increasing annual variation in daylength, the minimal shortening of the photoperiod perceived by plants occurs progressively earlier after the summer solstice. Many tropical herbs flower earlier at higher latitudes than conspecifics at lower latitudes (Ison and Hopkinson 1985). Conspecific trees of wide-ranging species should therefore flower earlier in the subtropics than in the tropics. Because of the six months difference in the zenithal position of the sun, flowering of wide-ranging conspecific trees in the Southern hemisphere should be six months out of phase with flowering in the north. In the proximity of the equator, flowering should be aseasonal.

**C6** - Flower induction occurs after the autumn equinox. At a latitude of 10°N in Costa Rica, where annual variation in daylength is ~ 1 h (Figure 1A), a relatively fast reduction in photoperiod of 15-20 min, probably large enough to be sensed by trees, occurs only around the autumn equinox. Allowing time for the perception of changes in photoperiod, the reprogramming of meristem identity genes from the vegetative to the reproductive mode, and the development of an inflorescence, flower buds should appear at the earliest in October, later if inflorescence development is slow or critical daylength is shorter than 12 h.

**C7** - Inflorescence development begins in the absence of distinct biotic or climatic cues. If anthesis is preceded or accompanied by developmental changes such as arrest of shoot growth, leaf shedding or bud break (Figure 1B 2, 5; Borchert 2000), or by distinct climatic change such as rain after drought, flowering may have been induced by these cues and photoperiodic flower induction cannot be inferred safely.

**Field sites, observed species and methods.**

*Field sites and climate.* Field observations were made at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica, the site of earlier studies of the phenology and ecophysiology of neotropical dry forest trees (Frankie et al. 1974, Reich and Borchert 1984, Borchert 1994a, 2000), and in areas between La Pacifica and Liberia, Lomas Barbudal, La Irma, and Tilarán. Monthly mean temperature is  $28 \pm 1^\circ \text{C}$  throughout the year. Normally, less than 5% of annual precipitation (range: 900 – 2100 mm) falls between Dec and Apr (Figure 1).

*Observed species.* Species observed in Guanacaste province (“observed species”) are listed in Table 1 and their flower development is described in Results. Methods of observation are described below. In the text, observed species and species cited from the literature will be referred to by genus name, unless several congeneric species are discussed. Papers listing authorities for species names are given in parentheses for Costa Rica (Frankie et al. 1974, Janzen and Liesner 1980), Mexico (Bullock and Solis-Magallanes 1990) and Bolivia (Justiniano and Fredericksen 2000).

*Identification of species with potential flower induction by declining photoperiod.*

After the first observations of synchronous flowering in many trees of *Calycophyllum* and *Cordia*, additional species with possible photoperiodic control of flowering were identified in several ways. First, all species flowering in Nov/Dec 1997 were recorded. Later, species with flower initiation between Oct and Dec were identified in records of tree phenology from Costa Rica, Mexico and Panama (Tables 1, 2; Frankie et al. 1974, Opler et al. 1980, Windsor 1982, Bullock and Solis-Magallanes 1990) and in records of flowering periodicity obtained from herbarium collections (Figures 3-5; Borchert 1986). Herbarium collections were examined for flowering periodicity (Figures 3, 5, 6) of all species with an observed or reported flowering period starting between Oct and Dec and their congeneric species.

*Screening of species by the criteria for photoperiodic flower induction.*

The criteria established above will be referred to as C1, C2, etc. throughout this paper.

*All observed species meet criteria C1, C4, C6, and C7.* In species selected for a flowering period which starts between Oct and Dec, flower induction takes place between Sep and Nov, i.e., after the autumn equinox and during a rainy period without notable climatic or phenological change (Figure 1). The selection procedure thus implies that all species meet criteria C6 and C7. Like the majority of tropical trees, and in marked contrast to most temperate trees, most tree species flowering between Oct and Dec have naked flower buds. The transition from vegetative to reproductive development can be therefore observed as easily as in herbaceous plants (Figure 2), and all species meet criterion C1. In contrast to flowering phenology in tropical rain forests, the large majority of dry forest trees, including the species listed in Table 1, flower every year (Frankie et al. 1974, Newstrom et al. 1994). For several species flowering of the same trees has been observed for 3-4 consecutive years (Figure 4; Table 2; Windsor 1982, Bullock and Solis-Magallanes 1990). Thus, all observed species are likely to meet criterion C4.

*Flowering synchrony among conspecific trees (C2).* For most observed species, in summer 1998 20 - 50 trees were identified, flagged with plastic tape and mapped (Table 1). To facilitate frequent observation, most trees were located along highways and country roads within 40 km of Hacienda La Pacifica. Tree locations ranged from moist and dry lowland sites to moist sites at elevations of  $\sim 900$  m within Guanacaste province. From Oct. 1, 1998 to the end of flowering in Feb. 1999 trees were monitored every 8 – 10 d. Shoot apices of small trees were observed directly, those of larger trees with the aid of binoculars. For each species qualitative and quantitative criteria were developed for recording flower development through anthesis. With few exceptions mentioned in the Results, the earliest stages of flower bud or inflorescence development were observed in all conspecific trees during the 10-d period given in Table 1.

Occasionally, an earlier initiation of reproductive development was inferred from the observation of a more advanced stage.

*Inter-annual variation in flowering time (C3)* can be assessed only from long-term flowering records, which are rare. Several consecutive, relatively short flowering periods with low inter-annual variation have been described for six species in Mexico, two species in Panama and three species in Bolivia (Figure 4; Windsor 1982, Bullock and Solis-Magallanes 1990, Justiniano and Fredericksen 2000). We established earlier that species-specific flowering periods obtained from sufficiently large numbers of flowering herbarium collections are similar to those observed in phenological field studies (Borchert 1996). The collections of the Herbario Nacional, San José, Costa Rica and the Missouri Botanical Garden, St. Louis, Mo., were used to analyze inter-annual variation in flowering periodicity. For each species, collection date and site of all flowering herbarium collections were recorded, and flowering periodicity was graphed (Figures 3, 5). Any abrupt increase in the number of flowering herbarium collections from one month to the next indicates low inter-annual variation in the onset of flowering and, implicitly, a regular environmental trigger of flowering (e.g., Figure 5 B,D; Borchert 1996). Several species flowering in Costa Rica between Oct and Dec 1997 were eliminated from the list of selected species, because flowering periods of herbarium collections were irregular or started many months before Sep. For most species listed in Table 1 herbarium collections were sufficiently large to establish low inter-annual variation of flowering periodicity with confidence (Figures 3, 5).

*Variation of flowering period with latitude (C5)* can be identified in herbarium collections of wide-ranging, well collected species (Figure 3) and by comparing flowering periods of species observed in the field at different latitudes in Mexico (20-23 °N: Table 2, Figure 4), Costa Rica (10 °N; Table 1; Figure 5 B,C) and Bolivia (18 °S, Figures 4, 5 D).

*Asynchronous flowering during the dry season.* Anecdotal evidence suggesting short-day induction of flowering in species which flower during the early dry season and do not meet the above criteria for photoperiodic control is described to encourage further observations and analysis.

*Observation of flower bud differentiation* To monitor the transformation of vegetative into flowering buds, shoot apices were collected from late Sep on until flower buds were clearly visible with the naked eye. Buds were fixed in FAA (formaldehyde-acetic acid-alcohol) and then transferred to 70% ethanol for observation in a stereomicroscope. In preparation for photography, buds were washed in 70% ethanol, dehydrated in an ethyl alcohol/acetone series (Cohen 1974) and critical-point dried using CO<sub>2</sub> (Crang 1988). No coating was necessary and photographs were taken with a Leica MPS 420 stereomicroscope and a Leica MPS 32 camera (Leitz, Wetzlar, Germany).

*Experimental suppression and induction of flowering in herbaceous plants* In Guanacaste the growing season of most herbaceous plants coincides with the rainy season and lasts from late May to Dec. Many herbs flower during the mid rainy season, but others were observed to flower synchronously in Sep/Oct 1997 during the late wet season. Flowering in these plants was therefore likely to be induced by declining photoperiod as in the observed trees. In late Aug 1998 we identified several patches of unknown grasses and herbs which were vegetative and thus likely to flower later. For each batch of plants, one set was left in place as a field control, and two sets of 8 – 10 plants each were transplanted into plastic bags with 2 L soil. One set of bagged plants was kept near the field lab under natural light conditions, the other set was exposed each day from 17:30 to 19:30 hrs to supplementary light from warm and cool-light 60-W fluorescent bulbs. As photoperiod declined and the time of dusk changed from about 18:20 to 17:40 hrs between Aug and Dec 1998, the extension of natural day-length increased from around 1 to 1.5 h (Borchert and Rivera 2000). Experimental plants were observed from Oct 1998 to Feb 1999.

**Table 1.** Observations on synchronous flowering in Guanacaste, Costa Rica. Species are ordered by time of flower initiation in Col. **b**. Content of columns: **a** – Species; \*) *C. candidissimum* in Costa Rica, *C. multiflorum* in Bolivia/Peru; **b - d** Field observations: **b** - 10-d period of synchronous appearance of flower buds; **c** – degree of synchronization of flower initiation (+++ - flower buds appear in >90 % of observed trees within 10 d; ++ - >75%); **d** – number of observed trees. **e- f** flowering periods obtained from herbarium collections in the northern (**e**) and southern hemisphere (**f**). **g** – References to phenological field observations (a – Borchert 1996; b – Frankie et al. 1974; c – Opler et al. 1980). **h** - Figures showing flowering periodicity of species.

<i>Species</i>	<i>Field observations</i>			<i>Herbarium</i>		Ref.	Figure
	Start	Synchr.	N	North	South		
<b>a</b>	<b>b</b>	<b>c</b>	<b>d</b>	<b>e</b>	<b>f</b>	<b>g</b>	<b>h</b>
A Herb: <i>Hyptis suaveolens</i>	9, 20-30	+++	>50	9-12	3-4		3G
B <i>Bixa orellana</i>	10, 1-10	+++	10	9-12	1-12	c	3B
C <i>Lonchocarpus minimiflorus</i>	10, 1-10	++	>50	5-11		b	5
D <i>Bauhinia unguolata</i>	10, 10-20	+++	>50	11-3	4-8	c	3A
E <i>Calycophyllum</i> *)	10, 20-31	+++	>50	10-1	3-6	a,b	3C
F <i>Luehea speciosa</i>	11, 1-10	++	>30	10-3		a,b	6
G <i>Luehea seemannii</i>	11, 1-10	++	>20	12-2		a,b	6
H <i>Cordia alliodora</i>	11, 10-20	+++	>50	11-2	4-8	a, b	3E
I <i>Ochroma pyramidale</i>	11, 10-20	+++	>20	10-2	5-8	b	3F
J <i>Cochlospermum vitifolium</i>	11, 20-30	+++	>50	12-4	5-10	a,b	3D
K <i>Gliricidia sepium</i>	12, 1-10	++	>50	11-4		b	7
L <i>Licania arborea</i>	12, 1-10	++	>20	12-2		b	7

## Results

### *Synchronous flowering initiation during the late rainy season in Costa Rica*

In marked contrast to the common and conspicuous flowering of leafless trees during the dry season (Figure 1, B 2,3), synchronous flower initiation between Oct and Dec always occurs in trees with a full crown of mature leaves. Several species-specific patterns of flower development were observed: (1) after several months of rest, the shoot apex resumes growth and changes from the formation of leaves to the formation of a terminal inflorescence (Figure 2 A-D); (2) resting axillary buds of all leaves on the current shoot start expanding and develop into axillary flowers or inflorescences; (3) a few resting axillary buds near the shoot apex start expanding and form an inflorescence; (4) during continuous, indeterminate shoot growth, shoot development changes from the formation of leaves to the formation of axillary flowers (Figure 2 E-F).

For the following descriptions of flower development, species are grouped according to their developmental pattern. For each species, the 10-d period during which flower buds became visible in most trees, the degree of synchrony and the number of observed trees are given in Table 1. Screening criteria supported by data sets will be given in parentheses as *C1*, *C2*, etc.

#### *Transformation of the apical meristem into an inflorescence*

*Calycophyllum candidissimum* (Rubiaceae; Table 1 E) is a common Central American pioneer species in degraded tropical dry forests, which produces large numbers of flowers every year. In late Sep all twigs had terminal vegetative buds protected by a cataphyll and located between two opposite leaves (Figure 2A). Four weeks later most twigs on mature trees ended in a characteristic set of three buds, the earliest stage in the development of the branched inflorescence (*C1,2*; Figure 2 B; Table 1 E). Synchronous flowering became very conspicuous in Nov-Dec, when the white bracts subtending the flowers covered the crown of all *Calycophyllum* trees throughout the landscape (Figure 3 C). Flowering of the congeneric *Calycophyllum multiflorum* in the southern hemisphere begins in Mar, i.e., 6 months out of phase with flowering in Costa Rica. Flowering of this species is highly synchronous and its flowering period varies little from year to year (*C2,3,5*; Figures 3 C; 4 C; Table 1 E).

**Figure 2.** Vegetative and reproductive buds of *Calycophyllum candidissimum* (A, B), *Cordia alliodora* (C, D) and *Bauhinia unguolata* (E, F). All 15-20 X.

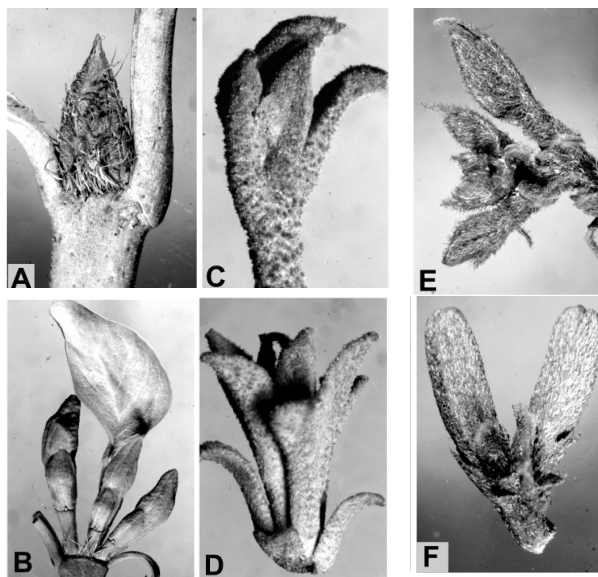
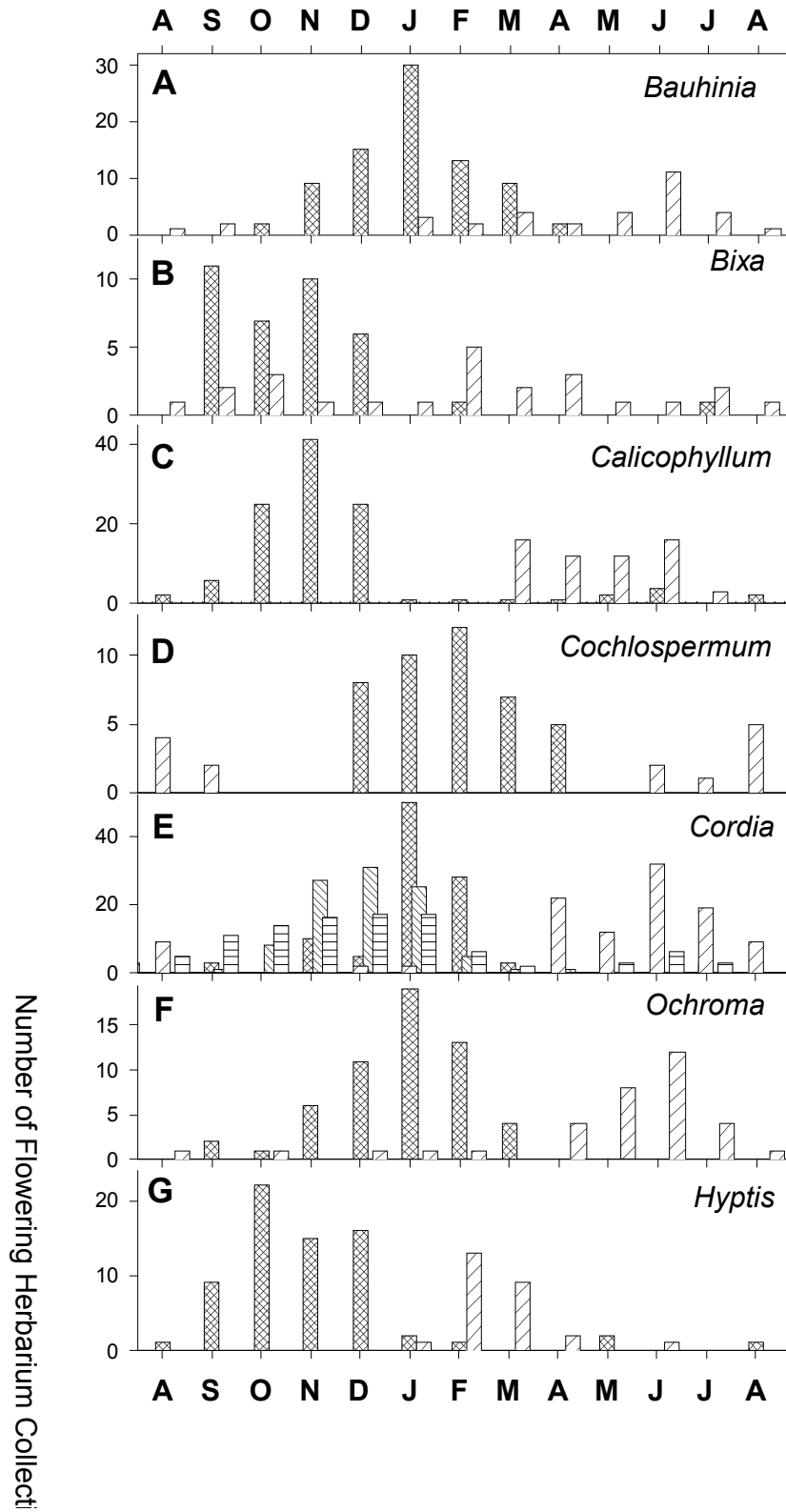


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**Figure 3.** Flowering periodicity indicated by flowering herbarium collections of six neotropical tree species (A-F) and one herb (G), which range from the northern to the southern hemisphere and start flowering soon after the autumn equinox (*vertical dotted lines*). Flowering times are based on collection dates and intensity of flowering on the number of monthly flowering collections in the herbarium of the Missouri Botanical Garden, St. Louis, Mo. Total number of flowering collections for the northern hemisphere (*cross-hatched bars*) and southern hemisphere (*diagonal hatching*), respectively, are given in parentheses after species names. A – *Bauhinia unguolata* (87,32). B – *Bixa orellana* (36,24). C – *Calycophyllum candidissimum* (Aug – Dec; 109); *C. multiflorum* (Mar-June; 15; *bars 4x*). D – *Cochlospermum vitifolium* (42, 21). E – *Cordia alliodora* (301;100). Geographical distribution of subpopulations: Mexico (20-22 °N) - *horizontal hatching*; Central America – *empty*; Panama (8 °N) – *cross-hatching*; Peru/Bolivia (10-18 °S) – *diagonal hatching*. F - *Ochroma pyramidale* ( 38, 32). G – *Hyptis suaveolens* (77, 26).

*Cordia alliodora* (Boraginaceae; Table 1 H) is a common pioneer species which ranges from Mexico to Bolivia and occurs in dry and wet forests. In late Oct, all twigs terminated in arrested, naked shoot tips with several leaf primordia (Figure 2 C). By mid Nov, many shoot tips of mature trees had developed into a triply branched flower bud (C1,2; Figure 2 D; Table 1, H). The growing inflorescence branched repeatedly and, starting in Dec, hundreds of small, white flowers gradually opened on the conspicuous inflorescence. The large number of flowering herbarium specimens collected throughout the geographical range of *Cordia* shows significant variation in flowering times with latitude (C5; Figures 3E; 4 A,B; Tables 1 H, 2 B). In subtropical Mexico (~20 °N) *Cordia* starts flowering in Sep, and with decreasing latitude flowering begins progressively later (Panama, 7 °N: Dec-Feb; Figures 3E; 4 B). In the southern hemisphere flowering starts in Mar/Apr, 6 months later than in Mexico (Figure 3E), and near the equator the species flowers throughout the year (Figure 4 F in Borchert 1996).

*Cochlospermum vitifolium* (Cochlospermaceae; Table 1 J) is a common dry-forest pioneer species. Because most trees are tall and slender, the shoot apex can be observed with binoculars only once the terminal inflorescence emerges above the surrounding foliage. In mid Dec all trees had terminal inflorescences bearing 10-20 flower buds, indicating that inflorescence development had started several weeks earlier (C2; Table 1 J). Flowers opened gradually over several months, and the rate of flower expansion varied widely with site water availability and the degree of leaf shedding. The abrupt increase in herbarium collections in Dec indicates low inter-annual variation in flowering initiation (C3; Figure 3 D). Similarly, in Northern Australia flowering of *C. fraseri* starts in June, soon after leaf fall, and has low interannual variation (Figure 3h in Williams et al. 1999).

*Bixa orellana* (Bixaceae; Table 1 B) is a large shrub with a conspicuous terminal inflorescence. The species is widely planted throughout the neotropics as an ornamental and as a source of a red food dye obtained from its seeds. We observed only a few flowering shrubs in the field. However, an abrupt increase of flowering herbarium collections in Sep indicates synchronous flower induction with low year to year variation (C2,3; Figure 3 B). In contrast to the distinct flowering periodicity in the northern hemisphere, none is evident in the southern hemisphere.

*Resting axillary buds develop into lateral flowers or inflorescences*

*Lonchocarpus minimiflorus* (Fabaceae; Table 1 C) is a common pioneer species in Central American dry forests. By late Sep 1997 and 1998 all buds in the leaf axils of current shoots had started to develop into small axillary inflorescences in the observed trees. During the following weeks flowers opened acropetally along the inflorescence (C1-4). Whereas flowering herbarium collections of the related species *L. robustus* and *L. acuminata* (Figure 5 A) show distinct, short flowering periods from Nov-Jan, flowering collections of *L. minimiflorus* indicate a flowering period 3-4 months longer than that observed in the field (Figure 5A).

*Ochroma pyramidale* (balsa; Bombacaceae; Table 1 I) is a common, fast-growing, evergreen pioneer species with very light wood. It ranges from Mexico to Bolivia and occurs in wet and dry forests. In all observed trees, by early Dec axillary buds of all leaves on the current shoot had expanded simultaneously into flower buds, whose growth was arrested when they attained a diameter of 1-2 cm (C1,2; Table 1 I). Flower buds resumed development later and expanded basipetally, one or two at a time, into large, conspicuous flowers. Beginning in Dec, anthesis lasted for several months. In contrast to the above species with continuous development from flower induction to anthesis, flower induction and early flower bud development in *Ochroma* are separated from anthesis by a rest period. The duration of this rest period varies from 1-2 weeks to several months with a bud's distance from the shoot tip. Herbarium collections show the extended flowering period from Nov - Mar and Apr - Aug in the northern and southern hemisphere, respectively (C5; Figure 3 F; Table 1 I).

*A few axillary buds near the shoot apex develop into inflorescences*

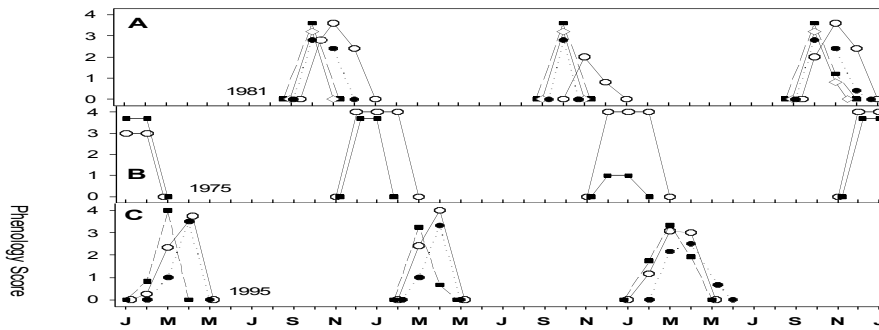
*Luehea speciosa* (Tiliaceae; Table 1 F). Several months after the arrest of shoot growth, 1-3 axillary buds near the shoot apex start developing into inflorescences bearing 10-20 flower buds. Flowers open gradually, one or two at a time, over several months. As flowering progresses, the number of flower buds in an inflorescence decreases and increasing numbers of wilted flowers and small fruits appear. Widely scattered trees of this brevideciduous species are notable only when bearing their conspicuous white flowers. For most trees monitoring therefore started after the opening of the first flowers, presumably at least 3-4 weeks after the beginning of inflorescence development. With the exception of a few trees observed in early Oct, most trees started flowering in early Nov for an extended flowering period (Table 1 F; Figure 5B).

*Luehea seemannii* (Tiliaceae; Table 1 G). Inflorescence development of this evergreen species is similar to that of *L. speciosa*. First flowers were observed in early Nov, when all observed trees were at the same early stage of inflorescence development. Field observations in Panama and flowering herbarium collections show a short flowering period which varies little between years (C2,3; Figures 4B; 5B).

*Licania arborea* (Chrysobalanaceae; Table 1 L) is an evergreen species belonging to a large genus of Amazonian rainforest trees. As in *Luehea*, inflorescences bearing many tiny flowers grow from 1-3 axillary buds near the shoot apex long after the cessation of shoot growth. In all observed trees fully grown, flowering inflorescences were present by mid-Dec, indicating flower induction in Nov (Table 1 L). An abrupt increase in flowering herbarium collections in Nov supports this conclusion Figure 5 C).

*Flower induction during indeterminate shoot growth*

*Bauhinia unguolata* (Caesalpinaceae; Table 1 D) is a small treelet (2-3 m) that colonizes degraded pastures and starts flowering when stems are only 1.5-2 m tall. Indeterminate shoot growth continues throughout the rainy season and is arrested during the dry season by increasing water deficits. Through late Sep the naked, hairy shoot tips contained a series of leaf primordia of increasing size (Figure 2E). During the first week of Oct, development of the growing shoot apex changed dramatically in all observed trees. Leaf primordia remained suppressed and prominent flower buds appeared (C1,2; Figure 2 F; Table 1 D). As shoot growth continued and new flower buds were formed at the shoot apex, older flower buds expanded, large flowers opened, and pod development began. By Dec the upper 30 to 50 cm of the growing terminal

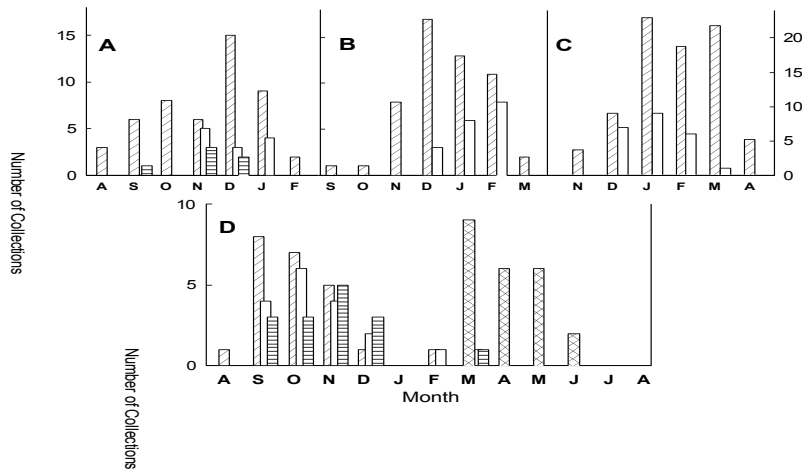


**Figure 4.** Flowering periodicity around the autumn equinox (dotted vertical lines: S – southern hemisphere; N – northern hemisphere) observed during three consecutive years in Mexico (A; data from Bullock and Solis-Magallanes 1980), Panama (B; Data from Windsor 1982) and Bolivia (C; Data from Justiniano and Fredericksen 2000). Phenology scores: 0 - no open flowers on any tree; 4 - all trees in full bloom. First year of observation is given near first flowering periods. Number of observed trees is given in parentheses. A - *Apoplanesia paniculata* (filled square; 50); *Cordia alliodora* (empty circle; 60); *Cordia elaeagnoides* (empty diamond; 26); *Heliocarpus pallidus* (filled circle; 38). B – *Cordia alliodora* (empty circle; 5); *Luehea seemannii* (filled square; 4). C – *Calycophyllum multiflorum* (empty circle; 12); *Centrolobium microchaete* (filled square; 12); *Pterogyne nitens* (filled circle; 6).

inflorescence contained all developmental stages from flower bud primordia to green and mature, brown seed pods. Flowering herbarium collections show the prolonged flowering period starting in Nov and May in the northern and southern hemisphere, respectively (C3,5; Figure 3 A).

#### *Periodic flowering near the autumn equinox in Mexico and Bolivia*

Published reports of flowering periodicity in the subtropics of Mexico (20-23 °N; Bullock and Solis-Magallanes 1990) and Bolivia (16-18 °S; Justiniano and Fredericksen 2000) complement our observations in Costa Rica. Over several years, distinct, short flowering periods of four Mexican and three Bolivian species occurred at the same time, at or shortly before the autumn equinox, and hence 6 months out of phase with each other (Figure 4, A,C). Even with the relatively low time resolution of monthly observations the sequence of flowering among the observed species is clearly preserved (Figure 4). Similarly, flowering herbarium collections of Mexican species show an abrupt increase in Sep (Figure 5 D). All 12 Mexican species, for which flowering data are available, start flowering in Sep/Oct, at least one month earlier than species observed in Costa Rica (Figures 4, 5 D; Tables 1 vs. 2). Three Bolivian species of *Vochysia* start flowering in Mar (Figure 5 D right).



**Figure 5** Flowering periodicity of selected species (*hatching* in parentheses) indicated by flowering herbarium collections (number in parentheses). A – *Lonchocarpus minimiflorus* (*diagonal*; 54); *L. robustus* (*empty*; 6); *L. acuminata* (*horizontal*; 12). B – *Luehea speciosa* (*diagonal*; 53); *L. seemannii* (*empty*; 17). C – *Gliricidia sepium* (*diagonal*; 82); *Licania arborea* (*empty*; 23). D - Mexican species: *Heliocarpus pallidus* (*diagonal*; 19); *Leucaena lanceolata* (*empty*; 24); *Ruprechtia fusca* (*horizontal*; 15). Bolivian species: *Vochysia hankeana* (*crosshatched*; 11).

#### *Asynchronous flowering during the early dry season*

Many species representing different flowering patterns flower during the early dry season (Figure 1 B-D). The following anecdotal evidence suggests short-day induction of flowering, but future observations are needed to support such a claim.

*Flowering after leaf abscission in the Leguminosae* (Figure 1, B 2,3).

*Erythrina* (coral tree, flame tree) is an unusually close knit pan-tropic genus of 108 species in the Fabaceae. Because of their spectacular, large (up to 50 cm long), red or orange inflorescences, many species are cultivated as ornamentals throughout the tropics (Lucas and Theobald 1982, Borchert 1986). The first flowers generally start expanding during leaf shedding, well before all leaves have abscised (Figure 1, B2; Figure 3 K-N in Borchert 1983). The majority of *Erythrin*as cultivated in the National Tropical Botanical Garden on the island of Kauai, Hawaii (18°N), start flowering in Nov/Dec (Figure 6, left; Lucas and Theobald 1982). As indicated by herbarium collections, in their native range most species start flowering in Nov-Dec and June-July in the northern and southern hemisphere, respectively (Figure 6). If, as in *C. alliodora*, flower induction and development of the large inflorescence prior to anthesis require at least 5-6 weeks, then flower induction is likely to occur in most species within 4 weeks after the autumn equinox and well before the beginning of leaf abscission. As only one or a few lateral buds near the shoot

**Table 2.** Synchronous flowering around the autumn equinox in Mexico. Field observations are from Figure 3 (referred to as \*3 in the Table) and Appendix in Bullock and Solis-Magallanes 1990. Flowering herbarium collections were examined at the Missouri Botanical Garden, St. Louis.

Species	Flowering months		Figure
	Field	Herbar	
<i>Apoplanesia paniculata</i> .	Sep - Oct	Jul - Dec	*3F
<i>Cordia alliodora</i>	Sep - Oct		3D, *3F
<i>Cordia eleagnoides</i>	Sep - Oct		*3F
<i>Heliocarpus pallidus</i>		Oct - Jan	8, *3F
<i>Leucaena lanceolata</i>	Sep - Oct	Sep - Nov	8
<i>Lonchocarpus constrictus</i>	Sep - Oct		*3H
<i>Lonchocarpus emarginatus</i>		Oct - Nov	
<i>Lonchocarpus lanceolatus</i>	Sep - Oct		*3I
<i>Lonchocarpus lineatus</i>		Oct - Nov	
<i>Lonchocarpus punctatus</i>		Sep - Oct	
<i>Luehea speciosa</i>		Sep - Jan	
<i>Ruprechtia fusca</i>		Sep - Jan	8

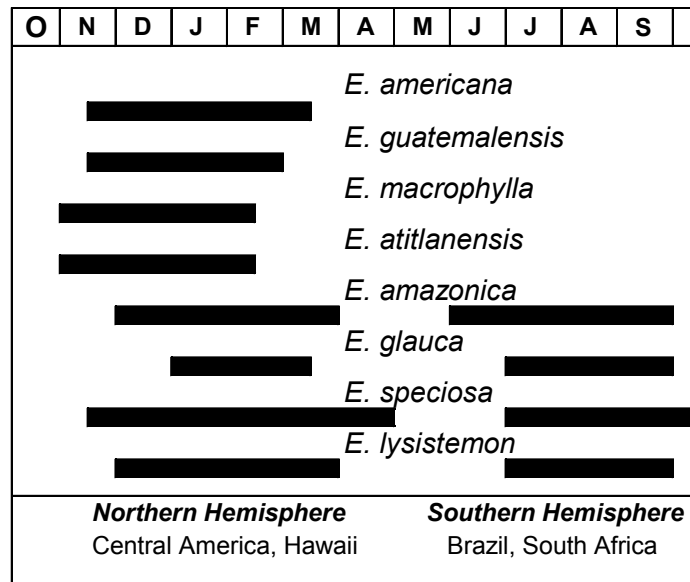
apex form inflorescences and several species flower while retaining their leaves (Lucas and Theobald, 1982), it appears unlikely that leaf abscission causes inflorescence development. *Erythrina poeppigiana* regularly exchanges leaves twice a year. Inflorescences develop during leaf abscission between Dec and Mar, but not during leaf shedding in Oct/Nov (Figure 3 K-N in Borchert 1983). During the prolonged flowering period of *Gliricida sepium* each axillary inflorescence starts expanding as soon as its supporting leaf has abscised. The first flowers were observed in mid Dec (Table 1 K) and flowering twigs were first collected in Nov/Dec (Figure 5C). Similarly, in *Caesalpinia eriostachys* and *Schizolobium parahybum* inflorescences started expanding on individual twigs immediately after partial leaf shedding in early Jan. As in *Erythrina* it is therefore likely that the resting flower meristems expanding after leaf abscission are induced earlier by declining photoperiods. As in the above species, axillary flower buds of *Myrospermum frutescens* normally expand after leaf shedding in Jan/Feb (Figure 1, B3; Borchert 1994a). Severe drought caused by the El-niño southern oscillation between June and Aug 1997 (Borchert, Rivera and Hagnauer, submitted) resulted in precocious leaf shedding of many trees of *Myrospermum* between Oct and Dec. Leaf shedding in Oct/Nov caused the expansion of lateral vegetative shoots, whereas leaf abscission in Dec was followed by expansion of axillary inflorescences.

*Axillary flowers on expanding shoots of Mimosaceae* (Figure 1, C2).

The leaf exchanging *Enterolobium cyclocarpum* regularly flowers on new shoots expanding shortly after leaf shedding in Feb/Mar (Figure 1 C2; Figure 3a in Borchert 1992). For several years, two trees growing at a wet site always exchanged leaves in Mar/Apr, 1-2 months later than all conspecifics, and consistently failed to flower. In summer 1998 many *Enterolobium* trees were defoliated by herbivorous insects. These trees flushed again between July and Aug, but did not form flowers on new shoots. In *Samanea saman* (= *Pithecellobium saman*) axillary flowers develop regularly on the first nodes of new shoots expanding in Feb/Mar, but not on the second flushes often formed during the wet season between June and July (Figure 8A in Borchert 1996). In 1997 abnormal drought delayed second flushes until Oct/Nov, when flowers developed on all new shoots. *Albizia guachapele*, which regularly exchanges leaves twice a year, flowers appeared on new shoots formed in Dec/Jan, but not on those formed in June/July.

*Terminal inflorescences in evergreen species* (Figure 1, C3).

The evergreen, leaf exchanging species *Anacardium excelsum* and *Hymenaea courbaril* normally form terminal inflorescences on shoots expanding after leaf abscission during the mid dry season (Figure 1, C3). As a consequence of abnormal drought, in 1997 these species exchanged leaves precociously in Sep/Oct (Rivera, Borchert and Hagnauer, submitted), but did not form terminal inflorescences on the new shoots. In *Cordia glabra* shoot growth in Jan/Feb regularly ends with the formation of a terminal inflorescence, but shoots expanding in June/July remain vegetative (Figure 3 G,H in Borchert 1983). In these evergreen species shoot growth thus ends with the formation of a terminal inflorescence when trees are exposed to photoperiods shorter than 12 h, but not under longer photoperiods.



**Figure 6.** Flowering periodicity of representative *Erythrina* species. Flowering period is based on herbarium collections from the species’ native habitats and on observations of flowering phenology of cultivated trees in the National Tropical Botanical Garden on Kauai, Hawaii (Lucas and Theobald 1982, Borchert 1986).

### *Photoperiodic induction of flowering in herbs*

Two broadleaved herbs (*Hyptis suaveolens*, Labiatae; *Achyranthes sp.*, Amaranthaceae) and several grasses (*Cynodon*, *Hyparrhenia*, *Panicum*, *Penisetum*, *Sporobolus*) were vegetative in late Aug and started flowering between Sep. 20 and Oct. 14, 1998 (*Hyptis*: Table 1 A). Flowering remained suppressed in plants potted in late Aug and exposed to a ~ 1.5 h daylength extension (17:30 – 19:30 hrs). When *Hyptis* and *Achyranthes* that had remained vegetative under experimental daylight extension were transferred to natural daylength in late Oct and Dec, flower buds appeared 4 weeks later. In a similar experiment, all *Hyptis* sown in Venezuela (8-10 °N) at monthly intervals from May to Aug flowered in Sep, even though plant height at flower initiation ranged from 180 to only 6.5 cm (Table 3 in Medina 1982). Herbarium collections of *Hyptis* indicate a start of flowering in Sep and Feb for the northern and southern hemisphere, respectively (Figure 3 G).

### **Discussion**

#### *Criteria to identify flower induction by declining photoperiod*

The screen used to identify flowering patterns indicative of flower induction by declining photoperiod is based on the assumption that regular, synchronous flowering after the autumn equinox must be induced by a reliable, annual environmental cue. Annual variation in day-length is the only environmental variable that meets this criterion and is perceived by plants. At low latitudes with annual variation in daylength of ~1 h, synchronous flowering after the autumn equinox therefore indicates induction of flowering by a decline in photoperiod of 30 min or less (Figure 1). This conclusion based on indirect evidence was confirmed experimentally by the suppression of flowering in herbaceous plants and in the tree *Hildegardia barteri* by >12.5 h photoperiods or night illumination (Njoku 1964, Hall et al. 1975).

Ideally the criteria for flower induction by declining photoperiod should be confirmed by biweekly field observations made in more than 10 conspecific trees at different latitudes for at least three years. It is unlikely that this will be ever achieved for any one, let alone several species. Observations of flowering periodicity in the common, wide-ranging pioneer species *C. alliodora* approach the ideal: there are field observations from three different latitudes for 3-4 consecutive years (Panama: Figure 4B; Costa Rica: Table 1; Mexico: Figure 4A) and >400 flowering herbarium specimens collected between Mexico and Bolivia (Figure 3 E; Figure 4 in Borchert 1996). These and other data confirm the good correspondence between flowering periodicity observed in the field and deduced from herbarium collections, as established earlier (Borchert 1996). Evidence for flowering periodicity documented by only relatively few herbarium collections or field observations is weak for individual species considered by themselves, but is strengthened by the observation of similar flowering patterns in several species from the same region (e.g., Figure 5 D) or genus (*Calycophyllum*, Figure 3C; *Lonchocarpus*, Figure 5 A, Table 2; *Luehea*, Figure 5 B) and by the availability of field observations and herbarium collections for any species (e.g., *L. seemanii*, Figures 4 B, 5 B; *Heliocarpus* Figures 4, 5 D). As a whole, the observations accumulated for more than 25 tree species flowering between Sep and Dec provide very strong indirect support for synchronous flowering with low inter-annual variation after the autumn equinox (C2, 3, 6; Figures 3-6; Tables 1,2) and for the predicted variation of flowering time with latitude (C5: Figures 3-6). These results imply that the proposed criteria are well suited to identify flowering periodicity indicative of photoperiodic control in field observations, published phenological records and flowering herbarium collections. In view of the small number of carefully executed multi-year phenological records of tropical dry forest species available for screening by the

proposed criteria, it is likely that many other species with photoperiodic control of flowering will be identified in the future.

#### *Validity of the screening criteria*

Because of our limited understanding of the control of flowering in tropical plants by very small changes in photoperiod (Thomas and Vince-Prue 1997), the evaluation of the proposed criteria for photoperiodic control of flowering and of the reliability of the supporting data must remain tentative. The postulated synchrony of flowering with low inter-annual variation (C2, 3) is supported by high resolution field observations (Table 1), short flowering periods with low inter-annual variation (Figure 4) and abrupt increases in flowering herbarium collections (Figures 3 B, D, G; 5 D). Synchronous flowering starts at different, species-specific times between Sep and Dec (Figures 3, 5; Table 1), i.e., the critical daylength varies between species, and in several species all conspecific trees in a landscape have the same critical daylength. *A priori*, there appears to be no compelling physiological or ecological reason why the biochemical mechanisms controlling the biological clock and critical daylength should not vary notably within tree populations. The scattered flowering herbarium specimens collected outside the principal flowering periods of several species (Figures 3, A-C, F, G) indicate that exposure to an inductive photoperiod is not an absolute prerequisite for flower induction, a fact established for many herbaceous species (Thomas and Vince-Prue 1997). Also, the gradual increase in flowering herbarium collections of several species (Figures 3A, C, F; 5) may indicate reduced synchrony of flowering initiation or moderate inter-annual variation in flowering time. Two sets of observations are particularly puzzling in this respect. In Costa Rica all observed trees of *L. minimiflorus* started flowering in early Oct during two consecutive years (Table 1), yet there are numerous flowering herbarium specimens collected in Central America between June and Sep (Figure 5A). In *Bauhinia* and *Bixa* flowering is notably more irregular in the southern than in the northern hemisphere (Figure 3 A,B), possibly because collections from South America include a larger fraction of samples obtained near the equator, where flowering is aseasonal (Figure 4 F in Borchert 1996: *C. alliodora* in Ecuador). Variation of flowering period with latitude (C5) was confirmed for a good number of species. Flowering periods in the northern and southern hemisphere are 6 months out of phase (Figures 3, 5 D, 6) and flowering starts consistently earlier in the subtropics than at lower latitudes, usually shortly before the autumn equinox (Figures 3 F; 4; 5 D; Tables 1 vs. 2). This implies that in subtropical species or subtropical races of wide-ranging species the critical daylength is slightly longer than 12 h.

#### *Analysis of different flowering patterns*

Declining photoperiod apparently induces different developmental changes in species with different flowering patterns. During continuous growth of the apical meristem morphogenesis of *Bauhinia* changes from the expansion of leaves with suppressed axillary buds to the suppression of leaf development accompanied by the release of lateral meristems from correlative inhibition and their differentiation into flowers (Figure 2 E,F). Implicitly, a set of genes controlling leaf development is turned off after the perception of inductive short photoperiods, while genes for flower differentiation are activated. In all other species which start flowering after the autumn equinox, declining photoperiod induces at least two distinct developmental sequences. First, arrested terminal or lateral buds are released from correlative inhibition by persisting old leaves and resume growth. This release from correlative inhibition is quite unusual, because arrested vegetative and flower buds normally resume growth only after leaf shedding or experimental defoliation (see below; Borchert 1991, 2000). Also, growth resumption in terminal buds (e.g., *Calycophyllum*, *Cochlospermum*, *Cordia*), a few apical lateral buds (*Licania*, *Luehea*) or all lateral buds on the current shoot (*Lonchocarpus*, *Ochroma*) must involve complex, species-specific changes in the positional control mechanism commonly referred to as apical dominance. Second, during growth resumption the meristems differentiate into an inflorescence (Figure 2, A-D) or, rarely, individual flowers



(*Ochroma*). In most species development appears to be continuous from the induction of a flowering meristem to anthesis, but in *Ochroma* lateral flower buds may rest for weeks before anthesis.

Synchronous flowering during the late rainy season is well suited to reveal flower induction by declining photoperiod, because flower induction and inflorescence development take place under favorable, relatively constant environmental conditions in the absence of other developmental changes (Figure 1, B1). In contrast, flower induction associated with specific phases of vegetative development is difficult to analyze, because the potential environmental and endogenous causes of flowering and vegetative development cannot be separately inferred from phenological observations (Figure 1, B 2-6, C 2-3). In several species flowering associated with leaf shedding, flushing or shoot growth cessation was observed between the autumn and spring equinoxes when days are shorter than 12 h, but not when days are longer (see Results). Photoperiodic induction of flowering meristems may therefore precede the flowering episodes observed under short days. This could be tested by defoliation experiments similar in design to the repeated sowing of tropical herbs, which reveals photoperiodic control of flowering (Results: *Hyptis*). Experimental defoliation of large branches of tropical trees during the rainy season usually induces bud break. For Fabaceae which flower during or after leaf shedding (*Erythrina*, *Gliricidia*, *Myrospermum*) the expansion of vegetative or reproductive lateral buds, respectively, after defoliation between Aug and Dec should reveal the time of flower induction and hence a possible role of photoperiod. For example, in two West African species lateral buds containing floral primordia develop in Oct, 4-5 months before anthesis in Feb/Mar (*Bosqueia angolensis*, *Monodora tenuifolia*; Njoku 1963). In the Mimosaceae and other families, presence or absence of flowers on new shoots induced by defoliation at various times of the year should reveal periods of photoperiodic induction of lateral or terminal flowers on growing shoots (see Results). The prevalence of specific flowering patterns in some families (Fabaceae: Figure 1, B2; Mimosaceae: Figure 1, B5, C2; Anacardiaceae, Boraginaceae: Figure 1, C3) illustrates the developmental and phylogenetic constraints imposed on the potential for photoperiodic flower induction by seasonal vegetative development. If photoperiodic control should be eventually confirmed in the above examples, then short photoperiods might be found to be involved in flower induction of many tree species flowering during the dry season in tropical forests (Figure 1; Frankie et al. 1974; Figure 1 C,D in Borchert 1998).

#### *Ecological significance*

In the tropics the zenithal position of the sun at the autumn equinox coincides with the location of the tropical inter-conversion zone and hence with maximum rainfall (Houston 1994). Declining daylength after the autumn equinox thus signals the approach of seasonal drought (Figure 1, A). Sensing the imminent end of the wet growing season is crucial for the optimization of reproductive effort in shallow-rooted herbaceous plants which desiccate and die during drought. In many tropical herbs declining photoperiods therefore induce flowering around the autumn equinox (Medina 1982, Ison and Hopkins 1985). For example, *Hyptis* often grows >1.5 m tall during the early rainy season, then flowers and produces abundant seed during the late rainy season until plants die when the topsoil dries out (Figure 3G; Medina 1982). Flowering after the autumn equinox is likely to optimize tree reproduction for similar reasons. Flowering is induced months after the cessation of seasonal vegetative growth, at a time when carbohydrate reserves are at a maximum and climatic conditions are favorable for inflorescence development and the completion of seed development before soil water reserves decline during the early dry season. It may be no coincidence that several of the species flowering during Oct/Dec are deciduous pioneer species producing large numbers of fast maturing seeds before the onset of seasonal drought (e.g., *Bauhinia*, *Calycophyllum*, *Cordia*, *Leucaena*, *Heliocarpus*). The geographical

distribution of species with flower induction by declining photoperiod also suggests that this flowering pattern may represent an adaptation to tropical climates with a long, severe dry season. Species flowering between Sep and Dec represent 16% of 130 tree species in a Mexican deciduous forest (Bullock and Solis-Magallanes 1990) and 12 % of 113 species in the semideciduous forests of Guanacaste, Costa Rica (Frankie et al. 1974), but only 2 of 189 species (1%) in the seasonally dry evergreen forest of Barro Colorado, Panama (Windsor 1982).

Since its discovery, photoperiodism has been recognized as an ingenious and reliable mechanism to optimize the timing of seasonal plant development in climates with a season unfavorable for plant growth and survival. Here, we present strong indirect evidence for flower induction in tropical trees by declining photoperiod. Elsewhere we will show that synchronous bud break and flowering of tropical trees during the late dry season, shortly after the spring equinox, are induced by increasing photoperiods (Borchert 2000, Borchert and Rivera 2000, Rivera et al. in preparation). The selection of temporal flowering patterns in tropical trees has been postulated to be driven by biotic interactions such as plant-pollinator interaction (Janzen 1967, Frankie et al. 1974, van Schaik et al. 1993, and many others). We see neither a compelling reason nor convincing observational evidence for the assumption that biotic interactions rather than seasonal variation in climate drive the selection of flowering periodicity controlled by rainfall periodicity or changing daylength (Figure 1).

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