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Phenology and flowering periodicity of Neotropical dry forest species: evidence from herbarium collections

ROLF BORCHERT

Department of Physiology and Cell Biology, Haworth Hall, University of Kansas, Lawrence, KS 66045-2106, USA

ABSTRACT. To examine the potential contribution of herbarium material to the description and analysis of tropical tree phenology, flowering times and geographical distribution were graphed for 1673 flowering collections from 18 species native to Neotropical dry forests and phenological differences between species were analysed. These include the timing and duration of flowering as well as morphological differences such as flowering on leafless twigs *vs* flowering on shoots bearing old or new foliage. Species-specific flowering periods of herbarium collections are similar to those observed in phenological field studies, but are often longer because of the larger geographical and temporal sampling range. Conspecific collections of different geographical origin show distinct differences in flowering periodicity, which are correlated with differences in the timing and intensity of the dry season. Interspecific differences in the timing of phenology relative to the dry season indicate differences in the control of phenology by seasonal drought. Herbaria thus represent a large potential source of phenological information which can either supplement and extend phenological field studies or provide phenological information for dry forest species not studied in the field but well represented in herbarium collections.

KEY WORDS: flowering periodicity, herbarium collections, Neotropics, phenology, tropical dry forest.

INTRODUCTION

Trees are the largest structural component and the dominant producers in tropical forests. Seasonal patterns of tree development have therefore a major influence on animal populations and ecosystem properties. The seasonality of tropical tree phenology is mainly determined by the duration and intensity of seasonal drought (Mooney *et al.* 1995, Murphy & Lugo 1986), because the annual variation in temperature and photoperiod is small at low latitudes. In marked contrast to cold-temperate forests where tree phenology is strongly synchronized by seasonal variation in temperature and photoperiod, seasonal climate and tree phenology are not well correlated in tropical dry forests characterized by 4–6 months of severe drought. Community peaks of shoot growth (flushing) and flowering occur either shortly after leaf shedding during the dry season or during the early rainy season, and phenological patterns differ widely between species (Borchert 1994b, Frankie *et al.* 1974).

There are only a few phenological field studies of dry forest species (e.g. Borchert 1980, Bullock & Solis-Magallanes 1990, Daubenmire 1972, Frankie *et al.* 1974, Lieberman 1982, Monasterio & Sarmiento 1976, Reich & Borchert 1984). The world's herbaria, which represent a vast potential source of phenological information on tropical tree species, have been utilized only occasionally to supplement phenological field studies (e.g. Borchert 1986, Mori & Prance 1986). This study explores how phenological information obtained from herbarium collections compares with the results of phenological field studies and how well it reveals phenological differences between species, temporal relations between phenology and seasonal climate, and phenological variation throughout a species' range.

The complex and indirect relations between seasonal drought and tree phenology have been unravelled only recently (Borchert 1992, 1994a,b, Holbrook *et al.* 1995). Increasing water stress during the early dry season generally causes a decline in water potential and induces leaf shedding. Rehydration of leafless twigs is a prerequisite for the subsequent opening of vegetative or flower buds. Variation of phenology between species and among conspecific trees is large under the same set of climatic conditions, because the timing of bud break during the dry season varies widely with the availability of water reserves in the soil or in tree trunks (Figure 1) and with species-specific responses to drought (Borchert 1994a,b). If the proposed causal relations between seasonal drought and tree phenology are correct, then species-specific phenological patterns should vary predictably with seasonal climate throughout a species' range and, inversely, should be biological indicators of environmental seasonality. These predictions will be tested with herbarium material of species whose ecophysiology and phenology are known from field studies and will be applied to species not analysed before.

MATERIALS AND METHODS

Herbarium collections of the Missouri Botanical Garden, St Louis, which specializes in Neotropical plants, were analysed. (In contrast to the common usage of the term 'collection', meaning 'an accumulation of objects', in taxonomic usage, adopted here, a 'collection' is material originating from an individual tree mounted on herbarium sheets.) Eighteen tree species native to neotropical dry forests were examined (Table 1). In selecting species for analysis, representation of different phenological patterns and the availability of herbarium collections, phenological field observations and ecophysiological data on seasonal water stress were considered.

For all flowering collections of a species, month of collection (= flowering month) and collection site (country and province) were recorded and the number of collections per month was tabulated and graphed for the species' entire range (Figures 2–8) as well as for specific countries or regions (e.g. Central America) represented by more than 20 collections (Figures 3, 4 and 7). Small

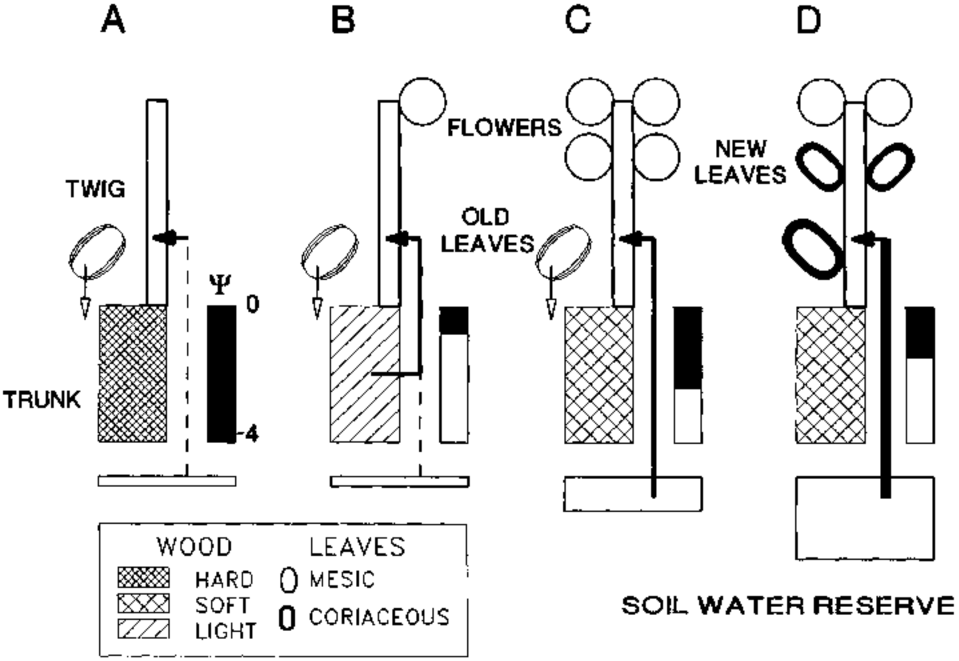


Figure 1. Differences in water relations and phenology during the dry season among tropical dry forest species. Soil water reserves (bottom), trunk water storage, a function of wood density (centre left) and leaf type determine the degree of desiccation during the dry season (gauges at centre right: stem water potential ψ in MPa) and the amount of water available for rehydration (arrows). Differences in the water status of the tree crown (twig) cause differences in phenology (top) as follows: A – After drought-induced leaf shedding hardwood trees at very dry sites are unable to rehydrate. B – In stem-succulent lightwood trees water storage in the trunk enables rehydration and sparse, prolonged flowering after leaf shedding. C – At savanna sites softwood trees rehydrate after leaf shedding and flower abundantly. D – At moist lowland sites softwood trees with coriaceous leaves rehydrate, flush and flower before or after leaf shedding (from Borchert 1994a).

collections from countries with similar climate and latitude were combined into sets of more than 20 (e.g. Colombia and Venezuela, Bolivia and Paraguay). Where possible, the time course of flower and fruit development was also evaluated (Figures 4D and 7).

RESULTS

Herbarium collections of flowering twigs contain several types of phenological information. Flowering periodicity throughout a species' range or for limited regions within that range can be obtained from collection dates and sites. The vegetative state of the shoot at the time of flowering is indicated by the presence or absence of leaves, and the timing of flowering relative to shoot growth can be deduced from the position of flowers on the shoot (terminal *vs* lateral flowers).

The species-specific flowering periods obtained from herbarium collections are generally similar to those observed in phenological field studies, but are often longer because of the much larger geographic and temporal sampling range (Table 1). The large interspecific variation in flowering times manifest

Table 1. Species of tropical dry forest trees analysed in this study. Flowering periods in Guanacaste, Costa Rica (Frankie *et al.* 1974), are compared with those obtained for Central America from herbarium collections. Species authorities are in Janzen & Liesner (1980).

Species	Family	Site *)	Flowering (months)		
			Costa Rica	Herbarium	Figure
Flowering of leafless trees during the dry season					
Bursera simarouba	Burseraceae	dry	4–5	4–5	2D
Cassia grandis	Caesalpinaceae	moist	2–3	3–5	8B
Cochlospermum vitifolium	Cochlospermaceae	dry	1–2	12–4	2C
Pseudobombax sp.	Bombacaceae	dry	1–3	12–3	2B
Spondias purpurea	Anacardiaceae	dry	1–2	1–4	2A
Tabebuia impetigunosa	Bignoniaceae	moist/dry	12–4	12–2	3
Dry season flowering on shoots bearing old leaves					
Calicophyllum candidissimum	Rubiaceae	moist/dry	11–1	10–1	5D
Cordia alliodora	Boraginaceae	moist/dry	1–2	1–3	4
Luehea seemannii	Tiliaceae	moist/dry	– –	12–2	6A
Dry season flowering on new shoots					
Anacardium excelsum	Anacardiaceae	riparian	2–3	1–5	5B
Guazuma ulmifolia	Sterculiaceae	moist	4–6	3–5	7
Pithecellobium saman	Mimosaceae	moist	4	2–5	8A
Thouinidium decandrum	Sapindaceae	moist	1–2	1–5	5A
Flowering during the wet season					
Apeiba tibourbou	Tiliaceae	dry	5–11	6–11	6D
Brosimum alicastrum	Moraceae	wet	– –	1–12	8C
Cedrela mexicana	Meliaceae	moist	6	5–8	5C
Luehea candida	Tiliaceae	dry	6	6–8	6C
Luehea speciosa	Tiliaceae	moist	12–1	9–2	6B

*) Observed in Guanacaste, Costa Rica (Borchert 1994b).
– – No data.

in herbarium collections (Figures 2–9) also agrees with the results of field studies (Frankie *et al.* 1974). Fourteen of the 18 species and the majority of all herbarium collections analysed flower during the dry season, but flowering periods are staggered such that at least two species flower during any month (Figure 9).

The following results illustrate the scope of phenological information obtained from herbarium collections and its interpretation. Descriptions of species-specific phenological patterns and Table 1 are ordered according to the flowering trees' vegetative status and the timing of flowering relative to the dry season, characters which provide cues as to the environmental control of phenology (see Introduction; Figure 1). To illustrate phenological similarities and differences, species are combined in the figures according to various common properties, such as stem succulence (Figure 2), terminal flowering (Figure 5), taxonomic similarity (Figure 6) or evergreen habit (Figure 8).

Flowering of leafless trees during the dry season

In trees flowering on bare twigs, future flower buds are formed and arrested at an early stage of development during shoot growth in the wet season. Bud development is resumed and anthesis occurs after leaf shedding during the dry season.

Stem-succulent trees with low-density wood are pioneers at dry upland sites. They rapidly shed their leaves during the early dry season. Water storage in the trunk enables maintenance of a high stem water potential and flowering during the dry season (Figure 1B; Borchert 1994a,b). In most species, flowers open gradually over 6–10 weeks during the early dry season (Figure 2A-C; *Cochlospermum*: Bawa & Frankie 1983), but *Bursera simarouba* flowers during the late dry season on emerging shoots (Figure 2D; Borchert 1994a,b, Stevens 1983). The flowering periodicity of herbarium collections throughout the species' range corresponds well to that observed in phenological field studies (Table 1), even though flowering periods of herbarium collections are longer because of regional and year-to-year variation in the onset of drought. There are distinct differences between the extended, early blooming of *Cochlospermum vitifolium*, the flowering period of *Spondias purpurea* and various species of *Pseudobombax* during the mid-dry season, and the late, short flowering period of *Bursera* (Figure 2). Reflecting the time course of the respective dry seasons, flowering in the southern hemisphere is about six months out of phase with flowering in the northern hemisphere (Figure 2B,C, downward bars).

Tabebuia impetigunosa is native to dry forests from Mexico to Argentina (Figure 3; Gentry 1992). At moist lowland sites in the dry forest of Guanacaste, Costa Rica, trees rehydrate and flower soon after the large, mesic leaves have been shed during the early dry season (Figure 1C; Borchert 1994c). The large, trumpet-shaped, purple flowers abscise within a week and pods begin to grow shortly thereafter. A second, rain-induced flowering episode may occur during the mid-dry season. Abundant, synchronized flowering of *Tabebuia* soon after drought-induced leaf shedding is reflected in the abrupt flowering peak during the early dry season followed by a tail representing later flowering episodes (Figure 3A,B), which are also documented by herbarium collections having both flowers and pods.

The availability of numerous collections from different regions throughout the range of *Tabebuia* permits the analysis of regional differences in the timing of flowering caused by variation in climate. The dry season and hence leaf shedding and flowering start earlier in Mexico than in Central America (Figure 3B,C, November–March). Flowering of a few Colombian collections in June, in addition to the main flowering period in December–February, reflects the characteristic bimodal rainfall distribution near the climatic equator (Müller 1967, Niewolt 1977). Flowering periodicity in the southern hemisphere generally concurs with the timing of the dry season (Figure 3A-D, May–October). Flowering peaks during the early dry season in collections from the Caatinga of central Brazil (Figure 3C), but the strong climatic variation in north-eastern Brazil (Niewolt 1977) results in irregular flowering throughout the year (Figure 3E). Flowering among trees at the southern end of the species' range, in the Andean foothills near Tucumàn, Argentina, is likely to be delayed by low temperatures

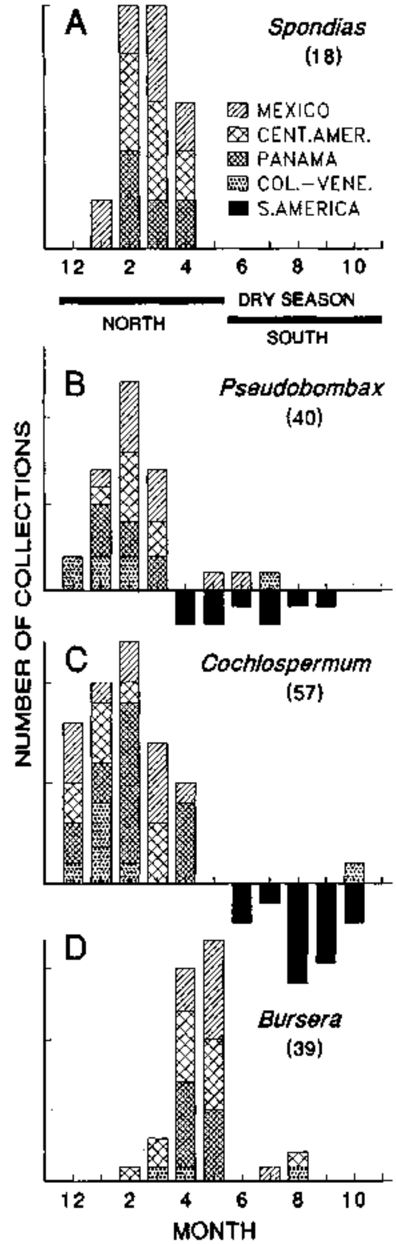
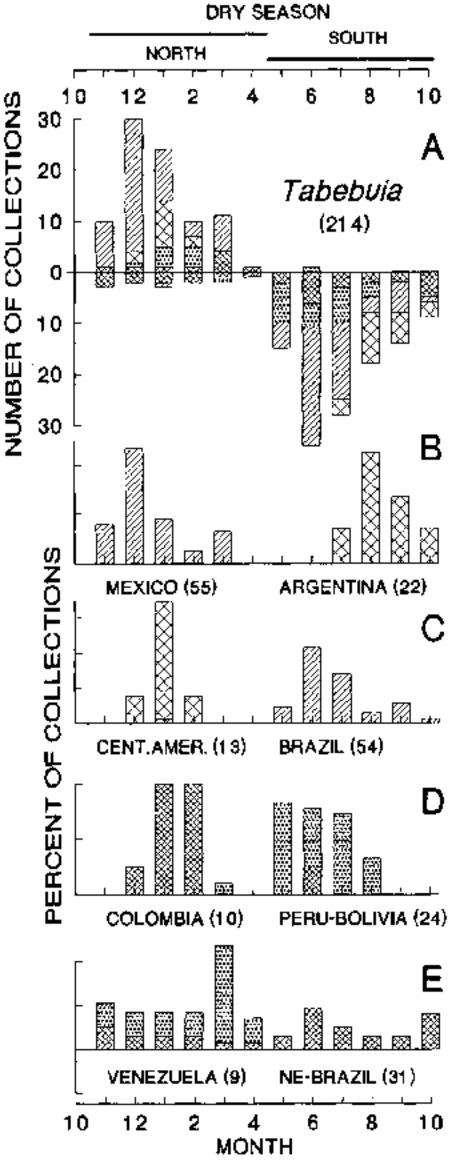


Figure 2. Flowering periodicity and geographical distribution of stem-succulent dry forest species with low density wood, which flower during the dry season after shedding their leaves. A – *Spondias purpurea.* Horizontal bars indicate the approximate duration of the dry season in tropical dry forests of the northern and southern hemisphere. B – *Pseudobombax ellipticum* (11), *P. septenatum* (17) and six other species (12). C – *Cochlospermum vitifolium.* D – *Bursera simarouba.* Stacked bars represent the number of flowering herbarium collections collected each month in the different regions indicated in the legend (CENT.AMER. – Central America; COL.-VENE. – Colombia, Venezuela; S.AMERICA = Brazil, Ecuador, Peru, Bolivia). Filled downward bars indicate flowering during the dry season in the southern hemisphere. Numbers in parentheses give the number of collections available for each species or genus. Intervals between tick marks on the Y-axis represent five collections.



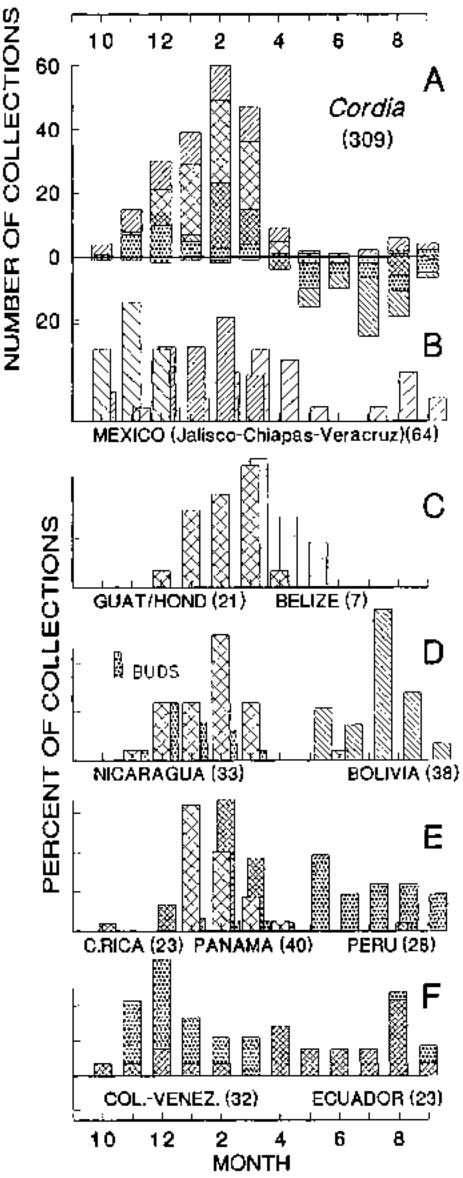


Figure 3. Left above. Flowering periodicity and geographical distribution of *Tabebuia impetiginosa*, which blooms during the early dry season soon after leaf shedding. A – Distribution of flowering herbarium collections by month of collection and region of origin in the northern hemisphere (November–April; bars up) or southern hemisphere (May–October, bars down). B–E – Percentage of collections flowering each month in different regions of the northern (left) and southern (right) Neotropics, ordered from B to E by decreasing distance from the equator (NE BRAZIL – north-eastern Brazil). Hatching in A corresponds to that in B–E. Interval between tick marks on Y-axis in B–E indicates 20%. Numbers in parentheses give available collections for the species (A) or for regions (B–F).

Figure 4. Right above. Flowering periodicity and geographical distribution of *Cordia alliodora*, which forms a terminal inflorescence during the early dry season on twigs bearing old leaves. Legends as in Figure 3 (GUAT/HOND – Guatemala, Honduras; C.RICA – Costa Rica; COL.-VENEZ. – Colombia, Venezuela). Dotted, narrow bars in D represent fraction of flower buds among flowering collections.

during the early dry season, which coincides with the southern winter (Figure 3B).

In *Cassia grandis*, an evergreen species of moist lowland sites in the dry forest biome, flower buds open on old wood and new shoots emerge soon after shedding of the drought-resistent, coriaceous leaves during the late dry season (Figure 8B; Borchert 1992, Irwin & Barneby 1982).

Dry season flowering on shoots bearing old leaves

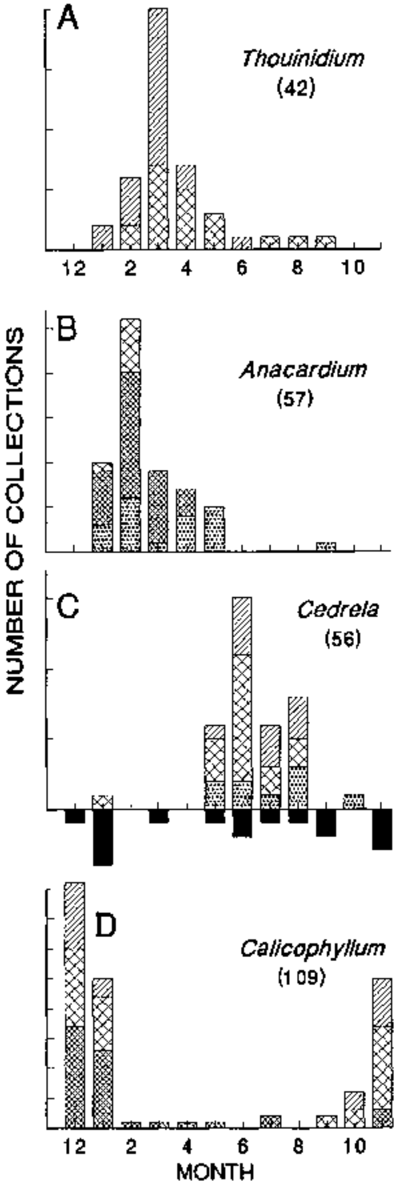
In *Cordia alliodora* (Opler & Janzen 1983) shoots formed during the early rainy season terminate in a naked, vegetative bud. Inflorescences bearing small flower buds are first observed at the tip of leaf-bearing shoots during the early dry season (Figure 4D left; Windsor 1982). As flowering progresses, the fraction of open flowers in the inflorescence increases (Figure 4D left). Flowering of individual trees lasts about 6–8 weeks and leaves are shed during or soon after flowering. Inflorescence formation in *Cordia* thus involves the resumption of shoot activity after a period of rest and the transition from a vegetative to a reproductive apical meristem during a period of increasing water stress.

In contrast to *Tabebuia* (Figure 3A), flowering frequency increases gradually in *Cordia* and flowering lasts more than five months in each hemisphere (Figure 4A) because of the temporal variations in the onset of flowering among regional collections which indicates differences in the timing and degree of drought. Throughout the northern range of *Cordia*, flowering starts earliest in regions with an early onset of severe drought (Figure 4B, October–December, Jalisco and Sinaloa provinces in Mexico; 4F, November–December, Miranda to Tachira provinces in Venezuela and Boyaca province in Colombia) and occurs latest in areas with moderate water stress during the dry season (Figure 4B, February–April, Veracruz province in Mexico; 4C, March–May, Belize; 4E, February–March, Panama). Flowering in Veracruz, Mexico, during the rainy summer (Figure 4B, July–September) represents an unexplained deviation from the periodicity observed elsewhere. Flowering generally begins during the early dry season of the southern hemisphere (Figure 4D,E, Bolivia, Peru). Flowering periodicity is indistinct, though slightly bimodal, in the proximity of the equator in Ecuador, where the occurrence of two annual dry seasons and the effect of topography on rainfall distribution result in considerable climatic heterogeneity (Figure 4F).

Like *Cordia*, *Calicophyllum candidissimum* and *Luehea seemannii*, growing at relatively dry savanna sites, form conspicuous terminal inflorescences during the early dry season, while retaining the old leaves formed during the early wet season (Figures 5D and 6A).

Dry season flowering on new shoots

In several species confined to lowland sites with root access to the water table, stem tissues rehydrate before or soon after leaf shedding and new shoots bearing lateral or terminal flowers develop during the dry season (Figure 1D;



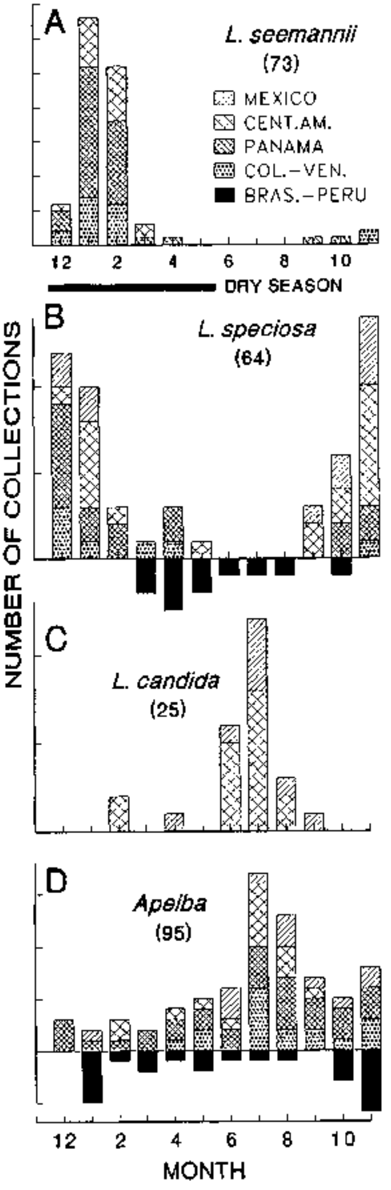


Figure 5: Left above. Flowering periodicity and geographical distribution of tree species forming a terminal inflorescence either shortly (A–C) or several months after flushing (D). A – *Thouinidium decandrum*. B – *Anacardium excelsum*. C – *Cedrela odorata*. D – *Calicophyllum candidissimum*. Legend as in Figures 2 and 6.

Figure 6: Right above. Variation in flowering periodicity among three species of *Luehea* (A–C) and the closely related *Apeiba tibourbou* (D), which form flowers on shoots bearing young (C, D) or several months old leaves (A, B). Legend as in Figure 2 (CENT.AM. – Central America; COL.VEN. – Colombia, Venezuela; BRAS.-PERU, Brazil, Ecuador, Peru).

Borchert 1994a,b). In the riparian species *Anacardium occidentale* (Hartshorn & Gentry 1983) and *Thouinidium decandrum* rapid leaf shedding during the early dry season is immediately followed by a short flush of shoot growth ending with the formation of a terminal inflorescence (Figure 5A,B). The drought-resistant, coriaceous leaves of *Pithecellobium saman* are shed during the mid-dry season and flowers open in the axils of immature leaves of shoots emerging soon after leaf fall (Figure 8A; Janzen 1983a).

In *Guazuma ulmifolia*, a common, wide-ranging pioneer species, the mesic, strongly desiccated leaves are retained long into the dry season, and lateral clusters of small flowers arise on new shoots emerging soon after leaf shedding during the late dry or early rainy season (Borchert 1994b, Janzen 1983b). In keeping with the wide variation in climatic conditions during the species' prolonged flowering period (Figure 7), the morphology of flowering shoots observed in the field and in herbarium collections varies widely. Trees flowering during drought bear flowers on short new shoots in the axils of small, immature leaves, whereas during the wet season inflorescences form in the axils of mature, relatively large leaves on long shoots. The development of small, green fruits, formed soon after flowering, remains arrested throughout the wet season (Figure 7C, August–November). Fruits resume development and mature during the early dry season (Figure 7C, November–March). Like flowering in *Cordia*, fruit maturation in *Guazuma* thus appears to be triggered by early drought.

Flowering periods of *Guazuma* are longer and geographical variation in flowering periodicity is greater than in most other species analysed. At higher latitudes, a single flowering period starts during the late dry season and extends well into the wet season (Figure 7B,C,G). At lower latitudes flowering becomes distinctly bimodal in some regions (Figure 7D,E,H), but not in others Figure 7F,I). As in *Tabebuia* and *Cordia*, flowering is aseasonal near the equator (Figure 7J). The periodicity of fruit maturation, which generally coincides with the onset of drought, is notably more distinct than flowering periodicity, particularly at lower latitudes where bimodal or aseasonal flowering is accompanied by seasonal fruit maturation (Figure 7D,E,H–J).

This relatively detailed analysis of flowering and fruiting periodicity in *Guazuma* illustrates the information obtainable for wide-ranging species for which large numbers of herbarium collections are available. The analysis of regional phenological patterns is clearly more reliable for regions with high sample numbers (Figure 7B–D,G) than for those represented by only few collections.

Flowering during the wet season

Luehea candida (Haber & Frankie 1983) is representative of other species of dry upland forests not included in this study. During the dry season such trees desiccate strongly, shed their leaves and then remain in a state of drought-imposed rest (Figure 1A; Borchert 1994b). The first rains of the rainy season trigger a short period of shoot growth ending with the formation of terminal flowers (Figure 6C). Occasionally, trees at wet sites flush and flower during the

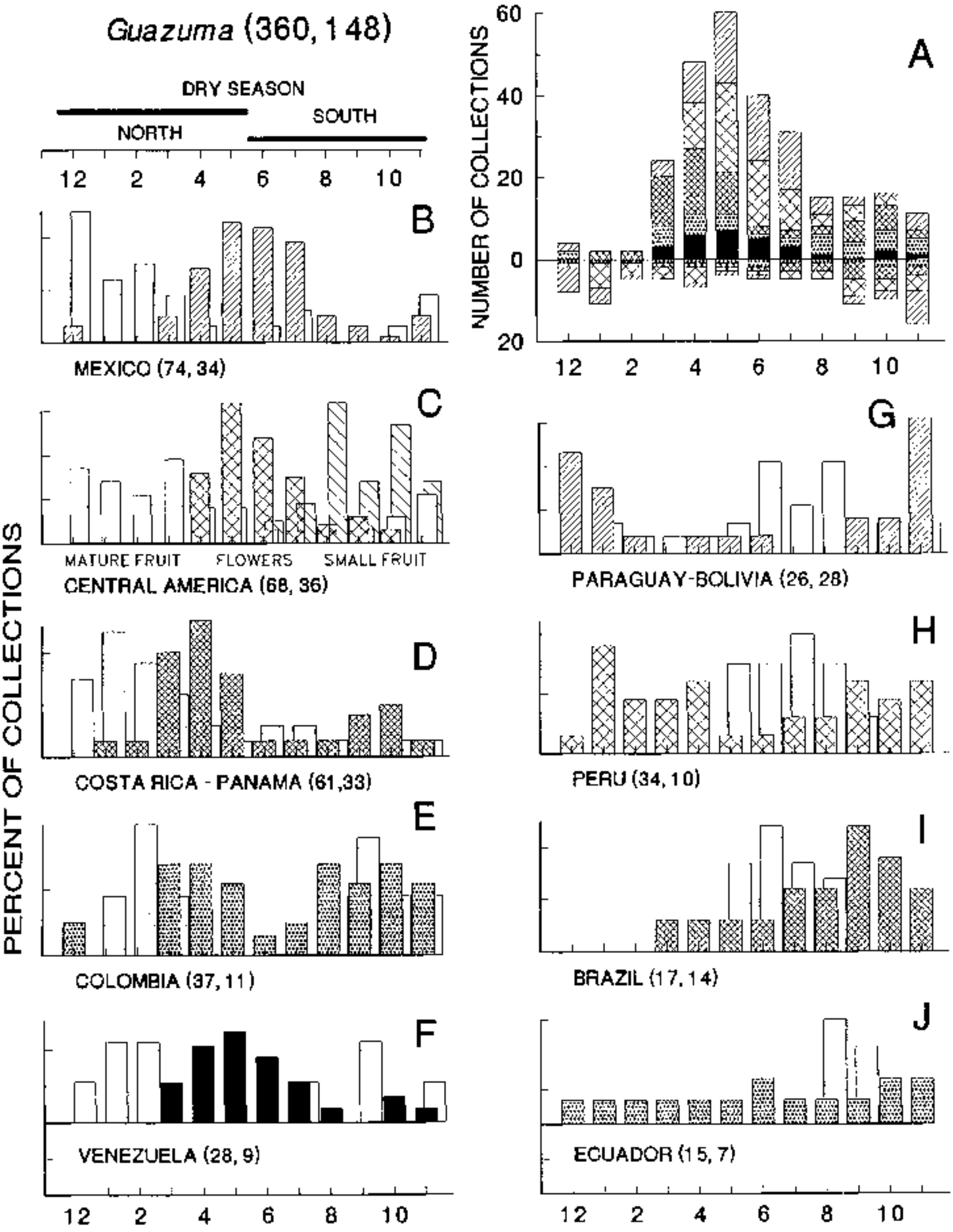


Figure 7. Periodicity of flowering and fruiting in *Guazuma ulmifolia*. Lateral clusters of flowers develop in the axils of young leaves. Early fruit development remains arrested throughout the wet season, and fruits resume growth and mature during the dry season (C). A – Distribution of flowering herbarium collections by month of collection and region of origin in the northern (bars up) or southern hemisphere (bars down). B–J – Percentage of monthly collections bearing flowers (different hatchings) or mature fruits (light dots; see C) in different regions of the northern (B–F) or southern Neotropics (G–J), arranged by decreasing distance from the equator. Hatching in A corresponds to hatching for flowering in B–J. Interval between tick marks on Y-axis in B–J is 10%. Numbers of flowering and fruiting collections, respectively, are in parentheses.

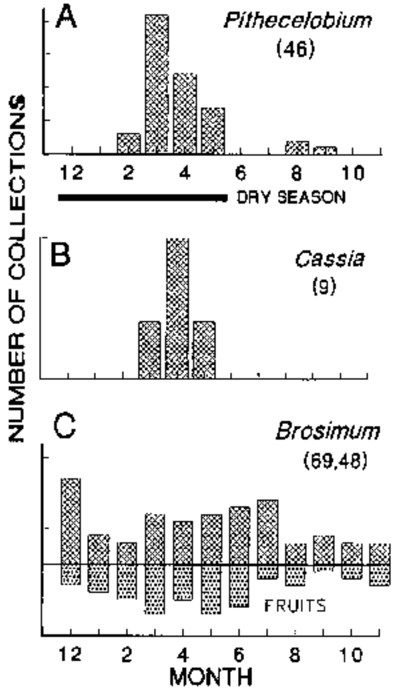


Figure 8. Flowering periodicity of evergreen species with coriaceous leaves growing at moist lowland sites, where roots have access to the water table. A – *Pithecellobium saman*; B – *Cassia grandis*; C – *Brosimum alicastrum*. Intervals between tick marks on Y-axis represent five collections.

dry season (Figure 6C, February–April). Although *Cedrela odorata* is a tree of moist lowland sites, it stands bare during part of the dry season and then flushes and flowers during the early rainy season (Figure 5C). As with other species, flowering periodicity of *Cedrela* is indistinct in the equatorial regions of South America.

Apeiba tibourbou forms flowers in the axils of young leaves during prolonged periods of shoot growth. At dry sites, trees are deciduous and shoot growth and flowering last for much of the rainy season (Figure 6D, June–November), but at wet sites shoot growth and flowering resume after leaf shedding and rehydration during the dry season (Figure 6D, December–May; Borchert 1994b). In contrast to the above species and somewhat like *L. seemannii*, development of the terminal inflorescence in *Luehea speciosa* begins after a period of arrested shoot growth during the late wet season (Figure 6B). Flowering periodicity thus varies widely among species within the genus *Luehea* (Figure 6A–C). *Brosimum alicastrum*, a riparian species of dry forests ranging from Mexico to Bolivia, is the only species analysed which flowers and fruits throughout the year (Figure 8C).

DISCUSSION

Potential and limits of phenological analysis

A good deal of phenological information can be obtained from herbarium collections of well-represented species (>30–40 collections) either directly (vegetative state of flowering shoots, flowering periodicity and its regional variation) or indirectly (time of leaf shedding or flushing relative to flowering). Although this information is not as complete and precise as phenological field observations, it clearly reveals characteristic differences in phenology between species and provides cues as to the environmental control of phenology (see below). In contrast to phenological field observations of small numbers of trees within a limited area, herbarium collections from a species' entire range reveal not only interspecific differences in flowering periodicity relative to seasonal drought, but also its variation throughout the species' range.

Most of the well-collected dry forest species analysed here are relatively small, wide-ranging trees, which are common in secondary forests of floristically well-studied countries (e.g. Mexico, Panama) and display conspicuous flowers for several weeks. Herbarium collections were found to be too small for phenological analysis for about half of the dry forest species analysed in earlier field studies and for the majority of the small sample of Neotropical rainforest species which was examined. Poorly represented species include both rare species and species for which flowering specimens are difficult to collect, such as large canopy trees and species flowering irregularly or for short periods.

Control of phenology by variation in tree water status

Phenological phase changes such as the initiation of shoot growth or flowering of tropical trees at specific times of the year are often thought to be 'triggered', i.e., to be controlled positively and directly, by the perception of an appropriate environmental cue (Ashton *et al.* 1988, Augspurger 1982). According to this reasoning any abrupt increase in the flowering frequency of a species, manifest in a maximum of flowering collections soon after the onset of flowering, should indicate induction of flowering by some environmental cue (Figures 2, 3, 5 and 6). Pronounced, one-month peaks should indicate the simultaneous opening of flowers in individual trees triggered by the same environmental cue throughout a given region or the range of a species (Figures 3B,C left, 5 and 6A,C).

In tropical dry forests, the most likely environmental changes controlling the periodicity of tree growth and flowering are the first heavy rainfalls after a period of severe drought or the cessation of rains. In strongly desiccated, leafless trees heavy rainfalls cause rehydration and the opening of resting flower buds or the expansion of new shoots and leaves (Borchert 1994c). Synchronized flowering on new shoots at the start of the rainy season thus indicates rain-induced shoot growth accompanied by the formation of lateral flowers (Figure 6D, July–November) or ending in a terminal inflorescence (Figures 5C and 6C). Flower formation on such shoots appears to be the indirect, endogenously controlled consequence of flushing and not a response to a specific environmental flowering cue (Borchert 1992). Rain-induced opening of preformed flower buds during the dry season (Augspurger 1982, Bullock 1986, Opler *et al.* 1976, Reich & Borchert 1982) is relatively uncommon and not represented among the species analysed here, because flowering collections of such species are rare.

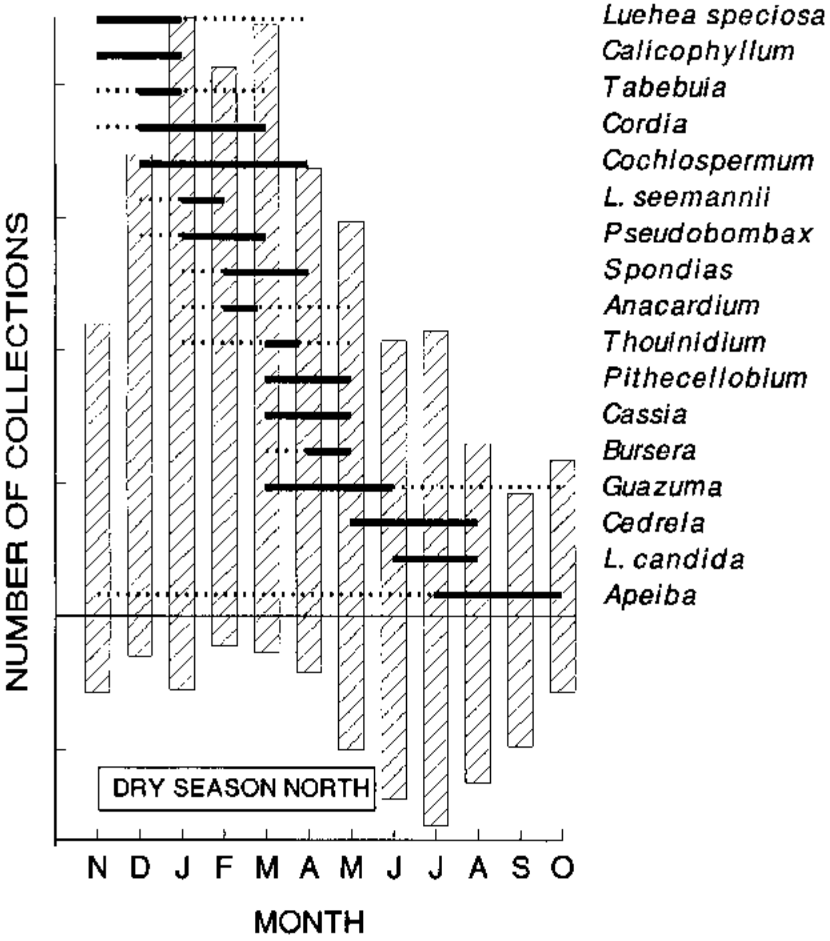


Figure 9. Monthly distribution in the northern (bars up) and southern hemisphere (bars down) of the 1673 flowering herbarium collections of 18 dry forest species analysed in this study (Figures 2–8). Horizontal lines represent flowering periodicity of 17 species in the northern hemisphere. Species were ordered by the first month of heavy flowering. Solid lines – main flowering period; dashed lines – low flowering activity. Tick marks on the Y-axis represent 40 collections.

In several species flowering frequency increases abruptly during the early dry season (Figures 2, 5A,B,D and 6A). Since water stress inhibits meristem activity, such synchronous flowering must be always the *indirect* result of drought-induced, rapid leaf shedding and subsequent rehydration which enables either the expansion of resting flower buds on bare shoots (Figures 1B,C, 2A–C and 3) or the emergence of new shoots ending in an inflorescence (Figures 1D and 5A,B). If drought-resistant leaves of trees at moist sites are retained well into the dry season, then flushing or flowering triggered by leaf fall occurs over an extended period and without temporal relation to any distinct environmental change (Figures 7 and 8A,B). In such species differences in drought resistance of leaves and in soil water reserves determine tree water balance during the dry season and hence, indirectly, variation in vegetative phenology which results in staggered flowering (Figure 7).

Formation of terminal inflorescences during the dry season on shoots bearing old leaves formed 4–7 months earlier (Figures 4, 5D and 6A,B) involves the resumption of growth in the shoot meristem after a period of rest as well as its transition from the vegetative to the reproductive state. This hard-to-explain, uncommon pattern of flowering raises questions that need to be explored in the future: How can shoot activity resume and an inflorescence develop on water-stressed twigs? What causes the transformation into a flowering meristem? Synchronized flowering of *Bursera* during the late dry season (Figure 2D) poses the opposite question: Why are, in contrast to other stem-succulent species (Figure 2A–C), flushing and flowering of leafless, presumably well-hydrated trees delayed until the late dry season?

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