Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2004) **13**, 409–425

RESEARCH PAPER

Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests

Rolf Borchert†*, Stefanie A. Meyer‡, Richard S. Felger§ and
Luciana Porter-Bolland¶

†Division of Biological Sciences, University of Kansas, Lawrence, KS 66045–7534, USA, ‡Las Delicias 11, Alamos, Sonora, Mexico, §Drylands Institute, PMB 405, 2509 North Campbell Avenue, Tucson, AZ 85719, USA, ¶Instituto de Ecología, A. C., Km. 2.5, Antigua Carretera a Coatepec 351; C.P. 91070 Xalapa, Veracruz, México. E-mail: borchert@ku.edu

*Correspondence: Rolf Borchert, Division of Biological Sciences, University of Kansas, Lawrence, KS 66045-7534, USA.
E-mail: borchert@ku.edu

ABSTRACT

Aim We analyse the proximate causes of the large variation in flowering periodicity among four tropical dry forests (TDF) and ask whether climatic periodicity or biotic interactions are the ultimate causes of flowering periodicity.

Location The four TDFs in Guanacaste (Costa Rica), Yucatan, Jalisco and Sonora (Mexico) are characterized by a 5–7 month long dry season and are located along a gradient of increasing latitude (10–30°N).

Methods To dissect the differences in flowering periodicity observed at the community level, individual tree species were assigned to 'flowering types', i.e. groups of species with characteristic flowering periods determined by similar combinations of environmental flowering cues and vegetative phenology.

Results Large variation in the fraction of species and flowering types blooming during the dry and wet season, respectively, indicates large differences in the severity of seasonal drought among the four forests. In the dry upland forests of Jalisco, flowering of leafless trees remains suppressed during severe seasonal drought and is triggered by the first rains of the wet season. In the other forests, leaf shedding, exceptional rainfall or increasing daylength cause flowering of many deciduous species at various times during the dry season, well before the summer rains. The fraction of deciduous species leafing out during the summer rains and flowering when leafless during the dry season is largest in the Sonoran TDF.

Main conclusions In many wide-ranging species the phenotypic plasticity of flowering periodicity is large. The distinct temporal separation of spring flowering on leafless shoots and subsequent summer flushing represents a unique adaptation of tree development to climates with a relatively short rainy season and a long dry season. Seasonal variation in rainfall and soil water availability apparently constitutes not only the proximate, but also the ultimate cause of flowering periodicity, which is unlikely to have evolved in response to biotic adaptive pressures.

Keywords
Costa Rica, flower induction, flowering phenology, Mexico, photoperiodic control, rainfall periodicity, tropical deciduous forest, tropical tree phenology.

INTRODUCTION

Annual repetition of consecutive developmental stages, collectively referred to as phenology, is a characteristic property of trees as large perennial plants. Seasonal patterns of development in forest trees, the dominant producers in terrestrial ecosystems, have a major influence on animal populations and ecosystem properties. In marked contrast to cold temperate trees, there is a large diversity of phenological patterns among tree species of tropical dry forests (TDF) characterized by a 5–7 month long dry season. Vegetative phenology varies with soil water availability during the dry season and ranges from evergreen species at moist or riparian sites to deciduous species at dry upland sites (Fig. 1a vs. 1d) (Borchert *et al*., 2002; Borchert, 1994a, 2003). Most tree species flower and form new leaves during relatively short periods (flushing), which vary among species of different functional types (Fig. 1). Flushing may be induced by the first heavy rains of the wet season (Fig. 1d), by leaf shedding during

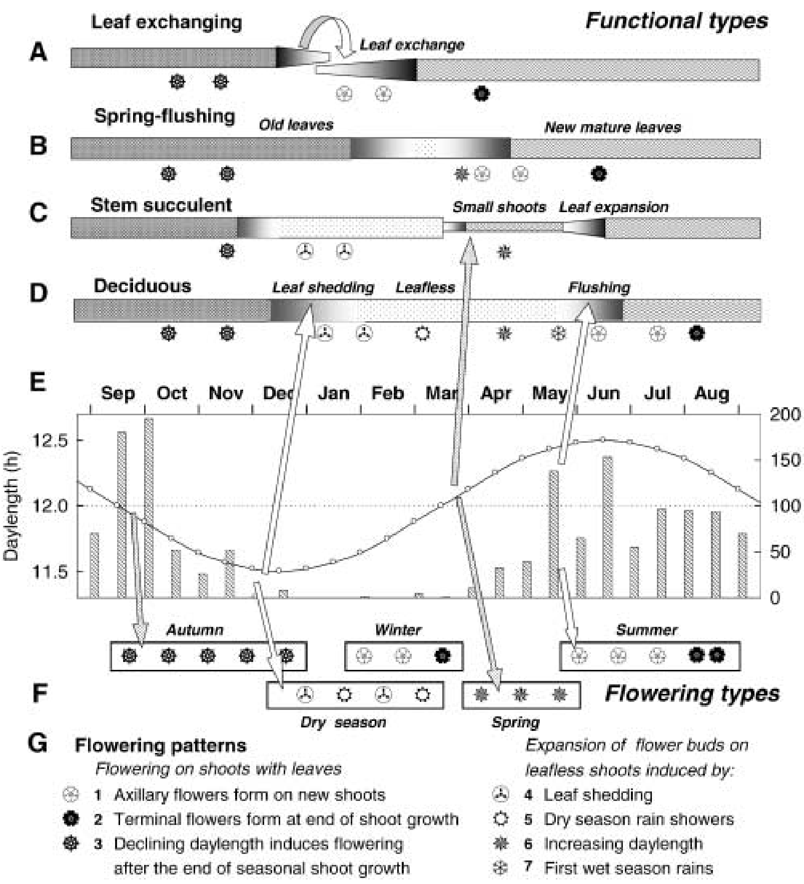

Figure 1 Vegetative and reproductive phenology of tropical dry forest trees. (A–D) Vegetative phenology in trees of different functional types and flowering patterns observed in different species during specific phases of seasonal development. (E) Annual variation in daylength and rainfall in Guanacaste, Costa Rica; (F) Flowering types with specific flowering periods caused by different environmental signals. (G) Flowering patterns observed in tropical trees. Arrows indicate environmental causes of vegetative phenology or flowering. Gradients of grey tones represent increasing or decreasing leaf area.

the dry season (Fig. 1a) or by increasing photoperiod after the spring equinox (Fig. 1b,c) (Borchert & Rivera 2001; Rivera *et al.* 2002). With declining annual precipitation, the fraction of evergreen species generally declines and forest physiognomy changes from evergreen to semideciduous or deciduous (Woodward, 1987; Neilson, 1995).

Seasonal distribution of species-specific flowering periods varies widely among five neotropical forests that are located along a gradient of increasing latitude (Fig. 2). In the evergreen wet forest at La Selva, Costa Rica, similar numbers of species flower during most months, i.e. there is no distinct seasonal variation in flowering periodicity at the community level (Fig. 2a). With declining annual precipitation and increasing severity of the dry season flowering periodicity becomes more distinct (Fig. 2b,c). In the semideciduous forests of Guanacaste, Costa Rica, and Yucatan, Mexico, about half of the tree species flower during the wet and dry season, respectively (Fig. 2b,c) (Frankie *et al.,* 1974; Porter-Bolland, 2003). In contrast, very few species bloom during the dry season in the deciduous forest of Jalisco (Fig. 2d, Nov–May) (Bullock & Solis-Magallanes, 1990), but the majority of species do so in the Sonoran TDF at the northern limits of the tropics (Fig. 2e) (Felger *et al.,* 2001).

The control of flowering periodicity in tropical forest communities is not well understood (Bullock, 1995) and it is not readily apparent how the observed large differences in flowering periodicity might be related to climatic differences among the five neotropical forests (Fig. 2). Recent analyses of the proximate controls of flowering in individual TDF species have shown that flowering periods are strongly determined by the timing of vegetative phenology and thus depend at least indirectly on environmental periodicity (Fig. 1) (Borchert, 1983, 1994a; Rivera & Borchert, 2001; Rivera *et al.*, 2002). Seasonal variation in climate should therefore be an important determinant of flowering periodicity at the community level (Fig. 2). On the other hand, the timing of synchronous flowering in individual species of tropical trees and, implicitly, the resulting flowering periodicity at the community level, are widely thought to have evolved as a result of biotic interactions between trees and their pollinators or seed dispersers (Wright, 1996). The potential adaptive advantages of synchronous flowering of leafless trees during the dry season, such as greater visibility of flowers by pollinators, have been discussed by Janzen (1967). The large differences in flowering periodicity observed among tropical forests in Costa Rica and Mexico therefore raise the question to what extent environmental periodicity or biotic interactions are the ultimate causes of flowering periodicity at the species and community level. Exploration of this question requires an understanding of the proximate mechanisms that control flowering time in individual tree species and presumably have been selected in response to environmental or biotic adaptive pressures.

Species-specific flowering periods are apparently determined by endogenous and environmental controls at several levels.

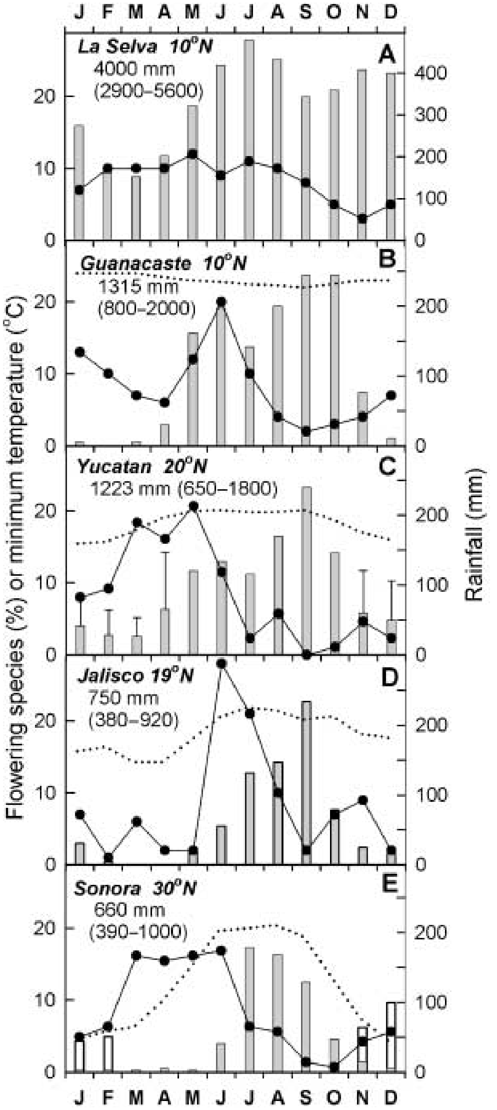

Figure 2 Seasonal distribution of the beginning of species-specific flowering periods (●), minimum temperature (·······), rainfall periodicity (histogram bars ▨), average and range (parentheses) of rainfall in the tropical rain forest of La Selva, Costa Rica (A; *n* = 185) and in the tropical dry forests of Guanacaste, Costa Rica (B; *n* = 98), Yucatan (C; *n* = 82), Jalisco (D; *n* = 103) and Sonora, Mexico (E; *n* = 122). In the Yucatan irregular rainfalls during the dry season result in large interannual variation (C, error bars). In Sonora about 4 out of 10 years have relatively high winter rainfall (E, ☐); in the remaining years there is only minimal rainfall between October and mid-June. *n*-number of species represented. Rainfall and temperature data from Frankie *et al*. (1974), Borchert *et al*. (2002), Porter-Bolland (2003), Bullock (1986b) and Estación climatológica San Bernardo (Sonora) and Zoh-Laguna (Campeche), Mexico.

Variation in the timing of flower induction and anthesis relative to vegetative phenology results in a number of characteristic 'flowering patterns' (Fig. 1g) (Borchert, 1983) (see Table 1 for definitions of terms relating to flowering phenology). Flowers may develop on foliated shoots during several stages of seasonal shoot growth: axillary flowers appear only on the first nodes of expanding shoots or throughout seasonal shoot growth, or shoot elongation ends with the transformation of the apical meristem into a terminal inflorescence (Fig. 1g1,2). The actual time of flowering on foliated shoots varies widely among species of different functional types with the time of flushing induced by different environmental cues (Fig. 1a, Jan–Apr; Fig. 1b, Mar–May; Fig. 1d, May–July). Flowering after seasonal shoot growth has ended may be triggered by various environmental cues. In some species of all functional types, declining daylength in autumn induces the highly synchronous development of lateral or terminal flowers during the late rainy or early dry season (Fig. 1a–d, Oct–Nov; Fig. 1g,3) (Rivera & Borchert, 2001). In many deciduous species, flower buds formed during the growing season remain dormant until bud expansion and anthesis are triggered during the dry season by rehydration of leafless twigs caused by leaf shedding, exceptional dry-season rain showers (Fig. 1c,d, Dec–Mar; 1g,4,5) (Opler *et al.*, 1976; Reich & Borchert, 1982; Bullock, 1986a; Borchert, 1994a, 2000; Porter-Bolland, 2003), or the first rains of the wet season (Fig. 1d, May; Fig. 1g,7) (Bullock & Solis-Magallanes, 1990). In other species, increasing daylength in spring induces highly synchronous flowering during the late dry season between March and May, weeks before the first rains of the wet season (Fig. 1b–d, Mar–Apr; Fig. 1g,6) (Borchert & Rivera, 2001; Rivera *et al.*, 2002).

In strongly seasonal tropical climates, careful phenological monitoring of at least 5–10 conspecific trees during 2–3 consecutive years permits deduction of the flowering cue from the time of synchronous flowering relative to seasonal variation in climate and photoperiod (Rivera & Borchert, 2001; Rivera *et al.*, 2002). Thus, flowering induced in leafless trees by isolated rain showers during the dry season (Fig. 1d, Feb–Mar) is synchronous among trees at a given microsite, but varies within a landscape with the patchiness of rainfall and between years with the timing of rainfall episodes (Reich & Borchert, 1982; Borchert *et al.*, 2002). The time of flowering induced by drought-induced leaf shedding (Fig. 1c,d, Dec–Jan) varies widely among individual trees in a landscape, with differences in soil water storage, and with the time of the last heavy rains of the wet season (Borchert *et al.*, 2002). At low latitudes, where annual variation in daylength is small and the critical daylength is generally close to 12 h, photoperiodic induction of flowering is indicated by highly synchronous flowering of all conspecific trees in a landscape after the equinoxes and by minimal variation in flowering time between years. Flower development on foliated shoots after the autumn equinox indicates flower induction by declining daylength (Fig. 1a–d, Oct–Nov) (Rivera & Borchert, 2001), and flowering of leafless shoots during the late dry season after the spring equinox indicates induction by increasing daylength (Fig. 1b–d, Mar–Apr) (Borchert & Rivera, 2001; Rivera *et al.*, 2002). Regular mass flowering of many Sonoran tree species during the late dry season is therefore induced by increasing daylength (Fig. 2e, Mar–May).

In this study we explore the feasibility of applying current understanding of the environmental controls of flowering in individual species to groups of species and entire TDF communities (Fig. 2). We postulate that the characteristic flowering

Table 1 Descriptions of flowering types based on field observations in the semideciduous forests of Guanacaste, Costa Rica and of Jalisco and Sonora, Mexico. Bottom: definitions of terms describing flowering phenology

Flowering type	Flowering period	Flowering cue	Flower morphology	Vegetative phenology	Representative species
Flowering on foliated shoots					
Summer species	During summer rains June–August	First heavy summer rains	Axillary or terminal flowers	Shoot and leaf expansion	*Luehea candida*
Autumn species	After autumn equinox September–December	Declining photoperiod		Mature leaves after end of flush	*Cordia alliodora*, *Cochlospermum vitiifolium*
Winter species	Mid dry season January–March	Drought-induced leaf shedding	Flowers from resting buds or on new shoot	During or after leaf exchange	*Thouinidium decandrum*, *Pithecelobium saman*
Expansion of flower buds on leafless shoots					
Dry season species	Soon after leaf fall or winter rains December–mid March	Leaf abscission or winter rain showers	Resting flower buds expand	Leafless hardwood or stem-succulent shoot	*Tabebuia* sp., *Caesalpinia eriostachys*
Spring species	After spring equinox, before summer rains Mid March–May	Increasing photoperiod	Flowers from resting buds or on new shoot		*Bursera* sp., *Plumeria rubra*, *Guazuma ulmifolia*
Early summer species	Soon after the first rains of the wet season June	First heavy rains			*Bursera* sp.

Definitions: Flowering type, Group of species that flower during a characteristic period on foliated or leafless shoots; Flowering pattern, The timing of anthesis relative to the annual cycle of vegetative phenology; Flowering period, The period during which flowering begins in an individual species or in all species of a flowering type; Flowering periodicity, The seasonal distribution of flowering starts among all species of a forest community.

periodicities observed in the four TDFs to be analysed represent the results of 'natural experiments', which reveal the environmental flowering cues that caused them. In the TDF of Guanacaste, Costa Rica, environmental control of vegetative phenology and flowering time of individual species results in five distinct 'flowering types', i.e. groups of species that flower during characteristic periods on current, foliated shoots or on leafless twigs formed during the previous growing season (Fig. 1f). These flowering types are analogous to the functional types of vegetative phenology, which comprise species with similar patterns of seasonal vegetative development (Fig. 1a–d) (Borchert, 1994a; Borchert *et al.*, 2002). Below we describe these flowering types and assign them the names of the seasons as a mnemonic aide. In the analysed TDFs the highest (summer) and lowest position of the sun (winter) coincide with the early rainy and dry season, and the autumn and spring equinoxes signal the approaching end of the wet and dry season, respectively (Fig. 1e).

Flowering types observed in the Guanacaste TDF (Fig. 1f)

Morphological details, simultaneous vegetative phenology and representative species are given in Table 1.

Summer flowering Flowering on young shoots formed during the summer rains.

Autumn flowering Synchronous flower development on foliated shoots with mature leaves is induced by declining daylength after the autumn equinox.

Winter flowering Flowering during the early dry season on new shoots formed in trees at moist sites soon after drought-induced leaf shedding.

Dry season flowering Expansion of resting flower buds is induced on leafless twigs during the early dry season by leaf shedding or isolated rain showers.

Spring flowering Synchronous flowering on leafless twigs is induced by increasing daylength during the late dry season after the spring equinox.

Throughout this paper the flowering types will be referred to as Summer species, Winter species, etc. As the characteristic flowering period of each flowering type is determined by a specific combination of vegetative phenology and environmental flowering cues, environmental flowering controls can, to a large extent, be deduced from flowering periods reported in descriptive phenological studies (see Results).

To examine the hypothesis that flowering periodicity has evolved primarily as an adaptation to increasing climatic periodicity we analyse the large differences in flowering periodicity observed among the four TDFs in several steps (Fig. 2). We first describe the identification of flowering types in phenological data sets of the four forests and determine the contributions of different flowering types to the observed flowering periodicity of each forest (Methods). We then apply current understanding of the proximate controls of flowering periodicity in individual species to the sets of species constituting the different flowering types and, lastly, to entire forest communities. Specifically, we examine the following predictions based on the hypothesis to be tested:

- flowering types similar to those observed in Costa Rica exist in other neotropical forests with a prolonged, severe dry season;
- the fraction of species in the different flowering types varies among TDFs with differences in climate, soil water storage and the fraction of species belonging to different functional types;
- the fraction of species in the various flowering types is therefore indicative of the predominant set of environmental conditions and of the contribution of different functional types to forest composition.

TROPICAL DRY FOREST CHARACTERISTICS

Climatic data and flowering periodicity for the following four TDFs are summarized in Fig. 2. General descriptions and a map showing the distribution of TDFs along the west coast of Central America and Mexico and in the Yucatan peninsula are available at the World Wildlife Fund's 'Wild World' Websites (WWF, 2001).

Guanacaste, Costa Rica

In the semideciduous lowland forests of Guanacaste (Frankie *et al*., 1974; Borchert, 1994a; Borchert *et al*., 2002) the distribution of tree species of different functional types (Fig. 1a–d) varies strongly with topography (see Introduction). Leaf-exchanging and spring-flushing species are restricted to riparian sites or moist upland sites with deep soil, and deciduous hardwood and stem-succulent species dominate dry upland sites with shallow soil. Canopy trees are generally 15–25 m tall.

Yucatan, Mexico

In the relatively flat, karst-like landscape of the Yucatan peninsula, which lacks permanent superficial rivers, local differences in forest vegetation are mainly determined by topographic variation in soil drainage (Porter-Bolland, 2003). On porous, well-drained calcareous soils most trees of the semideciduous forests are 10–20 m tall, emergents may reach 35 m, and the fraction of deciduous species varies from 25 to 75%. In the 'bajos' (large poljes or sinks) with poorly drained clay soils and a high water table, trees of the semideciduous forest range from 6 to 15 m. Up to 80% of all tree species occur in both habitats, but their relative abundance varies widely.

Jalisco, Mexico

In contrast to the other three TDFs, phenological observations in the deciduous lowland forest of Chamela, Jalisco (Bullock, 1986b, 2003; Bullock & Solis-Magallanes, 1990; Maass *et al*., 1995) were made almost entirely at dry upland sites with mean canopy height of 7 m and include only few species up to 15 m tall from moist arroyo sites. Correspondingly, 95% of the tree species are deciduous.

Sonora, Mexico

The TDF of Sonora, Sinaloa and SW Chihuahua, Mexico (Gentry, 1942; Robichaux & Yetman, 2000; VanDevender *et al*., 2000; Felger *et al*., 2001), is composed mainly of 10–15 m tall deciduous trees and represents the northernmost extension of this vegetation type. It is located in the foothills and valleys of the Sierra Madre Occidental, where it is protected from cold air masses penetrating from the north. Freezing temperatures limit the northern distribution of most tropical species. The areas occupied by TDF are therefore largely frost-free, and trees growing near the northern limit of their distribution may be shrub-like. The deciduous forest occupies an intermediate position between desertscrub and thornscrub (< 300 mm rain) and oak-pine woodlands and forests at elevations above 1000 m (Table 2). Within the TDF, water availability, and hence species distribution and phenology, varies widely with altitude (Table 2), topography (slopes vs. arroyos and river bottoms; north vs. south-facing slopes), and exposure to the moisture-carrying westerly winds. For example, during the dry season most trees at moist western locations of the Sierra Madre, which receive orographic rainfall, may still be green at a time when trees in dry valleys in the rain-shadow have lost most of their leaves (Table 2 and 450–600 vs. 600–800 m altitude). Arborescent cacti and stem succulent trees (*Ipomoea arborea*, *Bursera spp.*) prevail at very dry, rocky slopes; upper and south-facing slopes are generally dominated by leguminous species bearing compound leaves with very small leaflets (e.g. *Acacia* spp., *Lysiloma* spp.); large-leaved deciduous species (e.g. *Tabebuia impetiginosa*) tend to be confined to the lower slopes or arroyos; and evergreen species are found mainly along rivers or at arroyo bottoms (e.g. *Ficus* spp.; Table 2) (Gentry, 1942). Given this variation, it is impossible to know for which of the various microsites the rainfall measured in the TDF near Alamos is representative (Fig. 2e), but large differences in water availability among various sites can be deduced from the distribution and phenology of easily recognizable indicator species (Table 2).

METHODS

Identification of flowering types in phenological data sets

The identification of flowering types varies with the format of the descriptive phenological data being analysed. We first describe definitions of flowering types (Summer species, Autumn species, etc.) and their identification for Sonoran tree species and then adaptations of the method to the analysis of phenological data for Jalisco, Guanacaste and Yucatan.

Table 2 Vegetation transect and variation in dry forest phenology observed during the mid-dry season along the Pacific slope of the Sierra Madre Occidental from the Chihuahua-Pacific Railroad between Agua Caliente (Sinaloa) and Bahuichiva (Chihuahua)

Altitude (m)	Distance (km)	Vegetation type	Apparent soil water status	Phenology late January 2003				
				Legumes	*Ipomoea*	*Bursera*	*Tabebuia*	*Ficus*
240	0	Thornscrub	Very dry					
400–425	15–20	TDF	Very dry	0	0 F	0		
430	28	TDF	Dry	1	0 F	0		3
440	33	TDF	Dry–moist	2	0 F	1	0–1 F	3
450–600	40–50	TDF	Moist	3		2–3	3	3
800	55	TDF	Dry	1	0 F	0	0–1 F	3
1000	77	first pines	Moist	3				
1400	90	Pine-oak woodland	Dry					
1600	110	Pine-oak woodland						

Elevations and distances from Agua Caliente were obtained from *Maps and Guide to the Chihuahua-Pacific Railroad*. Observation sites were identified by km-markers along the track. Phenology: 0 – leafless; 1 – most leaves yellow; 2 – many leaves yellow; 3 – most leaves green; F – flowering. Indicator species: Leguminous trees, *Ipomoea arborescens*, *Bursera ssp*., *Tabebuia impetiginosa*, *Ficus* spp. For explanations see text.

Tropical deciduous forest in Sonora, Mexico

General phenological information for 122 species of trees and large shrubs from Sonora was obtained from Van Devender *et al.* (2000), Felger *et al.* (2001) and notes on phenology taken by S. Meyer from 1992 to 2002. Another 67 species were excluded from the analysis, because they are confined to the oak-pine forests at higher elevations (26), information on flowering phenology is imprecise or lacking (27), or trees flower at irregular intervals during much of the year and thus could not be assigned to any flowering type (14). For each species the following information was coded as given in parenthesis and entered into a spreadsheet (Appendix):

- species;
- family;
- flowering period;
- leaf phenology (Appendix, col. E: 1–early drought deciduous; 2–drought deciduous; 3–late drought deciduous; 4–leaf exchanging; 5–evergreen);
- water availability (Appendix, col. F: 1–species found at dry microsites; 2–arroyo or riparian species; 3–stem succulent);
- Habitat (Appendix, cols. G-I: Tropical dry forest, thornscrub, desertscrub);
- Diagnostic comments on phenology (e.g. 'mass flowering', 'flowering before appearance of new leaves', etc.), which are not shown in the Appendix. Starting month and duration of flowering as well as the start of mass flowering were obtained from the recorded flowering period (Appendix, cols. B–D).

As a first step in the identification of flowering types, all species were sorted by flowering start and leaf phenology (Appendix, cols. B, E). The final assignment of each species to a flowering type (Appendix, col. A) and the definition of the corresponding flowering period were guided by the criteria summarized in Table 1, as adapted to the specific climatic conditions and habitat distribution of Sonora. Columns containing decisive information are given in parentheses. In addition, diagnostic comments and information about flowering phenology from other sites as well as the authors' field experience were considered.

Summer species (Table 1, Summer species; Appendix, col. A *Su*). Flowering on foliated shoots during the summer rains (July–September).

Autumn species (Table 1, Autumn species; Appendix, col. A *Au*). Flower induction by declining daylength starts in September and ends in November/December (Rivera & Borchert, 2001). During the first months, flowers develop in the presence of mature leaves, but toward the end of the flowering period anthesis may occur on leafless shoots (e.g. *Cochlospermum*).

Winter species (Table 1, Winter species; Appendix, col. A *Wi*). Flowering on foliated shoots follows drought-induced leaf exchange during the dry season, which is limited to species growing at moist microsites (Appendix, col. E '4, 5', col. F '2'). Flowering generally starts within 2–3 months after the end of the summer rains (November/December) and ends in March.

Dry season species (Table 1, Dry season species; Appendix, col. A *Ds*). In Guanacaste and Jalisco, flowering on leafless trees is induced by leaf shedding within 1–3 months after the end of the wet season (Fig. 2c) (Appendix, col. E '1–2'), but mass flowering of leafless trees observed between December and February in several Sonoran Dry season species (Appendix, col. D) may be induced by the rather common winter rain showers (Fig. 2e). The separation of late-flowering Autumn species and early flowering Dry season species is somewhat arbitrary, because in many species differentiation of the resting flower buds, which later expand on leafless shoots, is induced during the late growing season by declining daylength (e.g. *Cochlospermum*, *Cordia*; Rivera & Borchert, 2001).

Spring species (Table 1, Spring species; Appendix, col. A *Sp*). Flowering of leafless trees (Appendix, col. E '2–4') starts around the spring equinox (mid March), the earliest time for which synchronous spring flowering induced by increasing daylength has been observed at low latitudes (Rivera *et al.*, 2002), and ends in mid-June before the summer rains. Because of the large number of spring flowering species in Sonora, stem succulent species of this flowering type (Appendix, col. F, *Sc*) were assigned to a separate type, Succulent spring species.

Early summer species (Table 1, Early summer species; Appendix, col. A *Es*). Rapid anthesis on leafless twigs is induced by the first summer rains before the emergence of new leaves. This flowering type, not observed in Guanacaste, is represented in Sonora mainly by species of Bursera, but is the major flowering type in Jalisco (see below). In the absence of precise field observations on the timing of bud break of flower buds relative to the first rainfalls in late June and to the beginning of leaf expansion, the assignment of June–flowering species to Spring species vs. Early summer or Summer species is somewhat arbitrary.

Many species of the Sonoran TDF occur also in the adjacent drier vegetation types (thorn- and desert scrub) and some species in the Appendix are restricted to these habitats (Appendix, cols. G-I). To analyse the distribution of flowering types in these and other subpopulations, their flowering periodicities were obtained from the Appendix by sorting for the columns given in parentheses and graphed: (1) mass flowering species (Appendix, col. D); (2) species occurring only in TDF or in thorn- or desert-scrub (Appendix, cols. G-I); (3) in addition, flowering periodicity of all Sonoran and Central Mexican cacti was obtained (Valiente-Banuet *et al.*, 1996; Paredes-Aguilar *et al.*, 2000).

Tropical deciduous forest in Jalisco, Mexico

Phenological observations were made biweekly between 1981 and 1984 in > 1000 trees of 108 species by Bullock & Solis-Magallanes (1990). Their Appendix provides the following information on flowering phenology for the 103 species analysed here: mean date of peak flowering (mo/d), mean duration of flowering episodes (mo), mean peak intensity of flowering (range 0–4) and the mean degree of foliation at the initiation of flowering (range 0–4). These data were entered into a spreadsheet and sorted by peak flowering date and leaf score (not shown). The month including the peak flowering date was used as month of first flowering.

In contrast to the other 3 TDFs, in Jalisco there are no species with flowering peaks in April/May, which can be unambiguously identified as Spring species. Instead, the large majority of species flower after the first heavy rains (Fig. 3c June). Species flowering in June with few or no leaves (leaf score < 1.5) were classified as Early summer species (Table 1; Fig. 3c Early summer species). This large flowering type has no equivalent in Guanacaste, where deciduous Dry season and Spring species flower at the height of the dry season, between January and April. Species flowering in June/July on foliated shoots (leaf score > 3) were classified as Summer species.

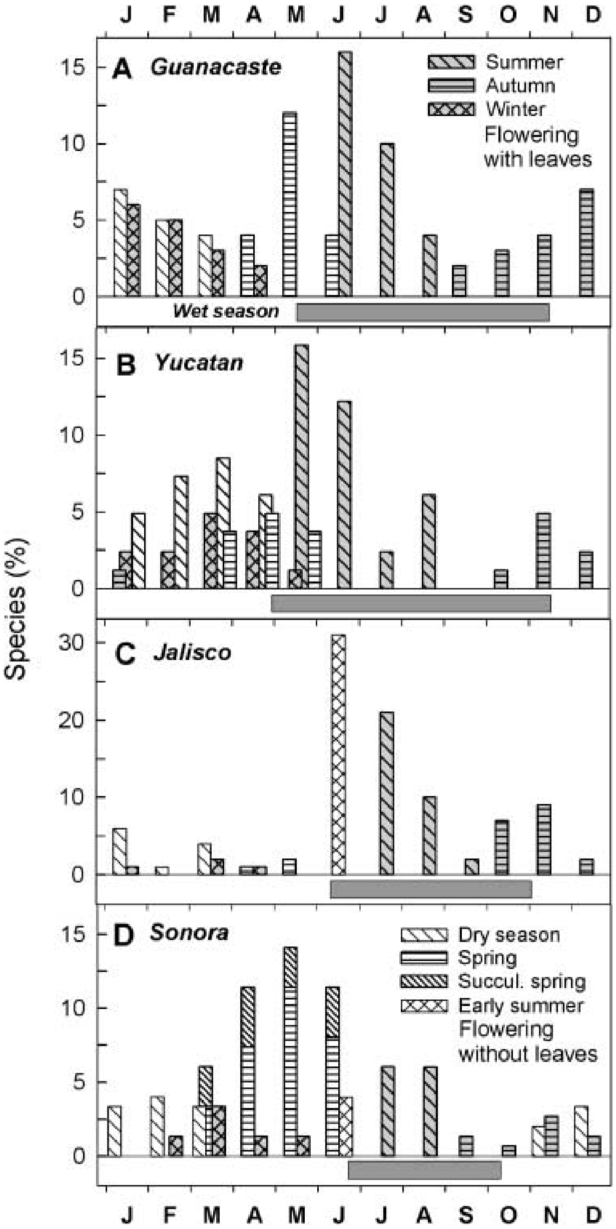

Figure 3 Contribution of different flowering types (Summer, Autumn, etc.; see Table 1; Figure 1f) to the flowering periodicity observed in the TDFs of Guanacaste (A), Yucatan (B), Jalisco (C) and Sonora (D). For explanations see text.

Tropical semideciduous forest in Guanacaste, Costa Rica

The phenology of 1137 trees in 113 species of the semideciduous forest of Guanacaste, Costa Rica was observed monthly between April 1969 and July 1970 (Frankie *et al.*, 1974). List 3 of the study provides the periods of leaf shedding or leaflessness, leaf flushing and flowering. Fifteen mostly evergreen, riparian species were excluded from this analysis, because phenological information was incomplete or flowering was prolonged and irregular. For the 98 analysed species, phenological information was entered into a spreadsheet (not shown), flowering on foliated vs. leafless

Table 3 Flushing and flowering periodicity of shrubs and treelets in the tropical semideciduous forest of Guanacaste, Costa Rica (data from Opler *et al.*, 1980)

	No. of species	
	Flushing	Flowering
Duration		
> 5 months	81	57
1–4 months	12	36
Starting time		
April–May	16	17
August–December	3	22

shoots was identified by comparing the first month of flowering with the time of leaf shedding or flushing, and species were then sorted by flowering start and leaf phenology. Our own observations of vegetative and flowering phenology in more than half of the analysed species allowed for extensive cross-checking during the assignment to flowering types according to the criteria given in Table 1.

In addition to the above phenological observations for trees, the phenology of 95 species of treelets and shrubs of the Guanacaste TDF has been described (Opler *et al.*, 1980). Almost 90% of these species flush during irregular periods over more than 5 months and only 40% of the species have distinct, brief flowering periods (Table 3). Establishment of flowering types for these species is therefore not feasible and the phenological observations were not combined with those for trees graphed in Fig. 3(a). However, these shrub species were included in the comparison of species occurring in more than one of the four forests (Fig. 4), because many of the species with distinct, brief flowering periods occur also in Jalisco.

Semi-deciduous forest in Yucatan

As part of a study of honey production in Yucatan, flowering periods and vegetative phenology of 88 tree species visited by honey bees were observed every 15–30 d between November 1998 and June 2000 in Montaña, Campeche, Mexico (Porter-Bolland, 2003). These species represent approximately 60% of all tree species in the area. Phenological information on interannual variation of rain-induced flowering during the dry season was obtained from local beekeepers, who are keenly aware of temporal changes in the major sources of nectar and pollen. Tree species were assigned to flowering types as described above. There is considerable overlap between the flowering periods of Dry season and Spring species (Fig. 3b), because irregular rain showers during the dry season (Fig. 2c) often delay leaf shedding and cause rain-induced flowering in leafless trees. Some wide-ranging species were classified as Spring species based on flowering patterns observed in Guanacaste (Fig. 5 Spring species), others because, in contrast to Dry season species, flowering was accompanied by the expansion of new shoots.

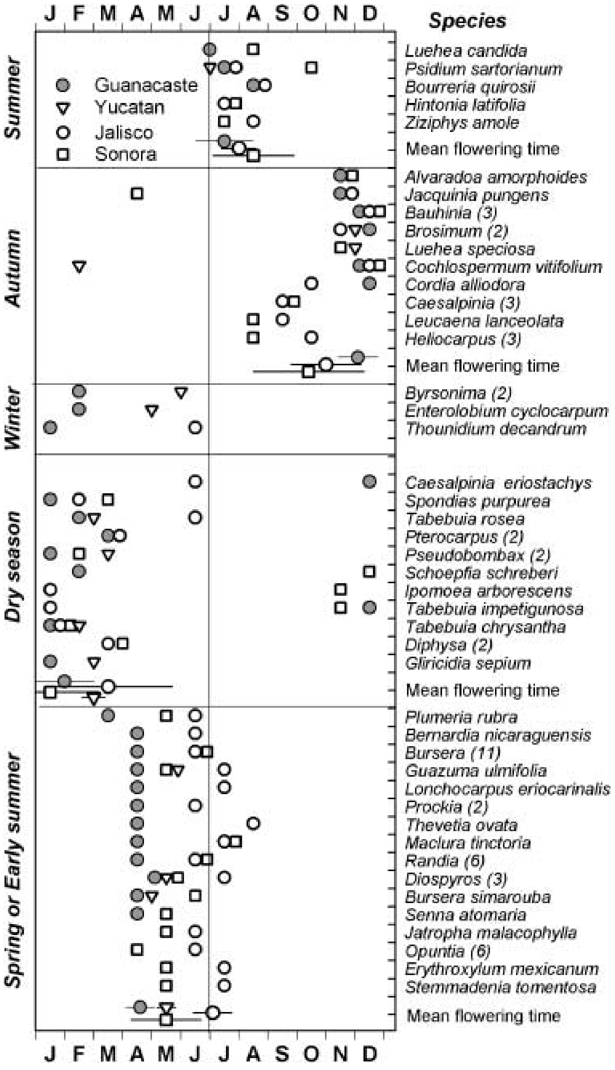

Figure 4 Flowering start for species or genera (right; number of included species in parentheses) occurring in more than one of the four analysed TDFs (see legend). Left *Y*-axis: Flowering types. For each flowering type with five or more species, mean flowering start date is given below the species-specific flowering times.

Comparisons among the four forests

To facilitate comparison of flowering periodicity among the four analysed forest communities, the fraction of species and means of flowering times in each flowering type were summarized for the four forests in Table 4. Means for flowering periods ranging from October to January were calculated by assigning '13' to January. We refrain from statistical comparisons of species number and mean flowering times among flowering types. The major differences among the four forests are self-evident without statistics and minor differences are irrelevant because of the ambiguity involved in assigning some species to a flowering type (Table 4; Fig. 4). To identify the variation in flowering times among species or genera represented in more than one of the forests, the species lists of the four forests were combined and sorted

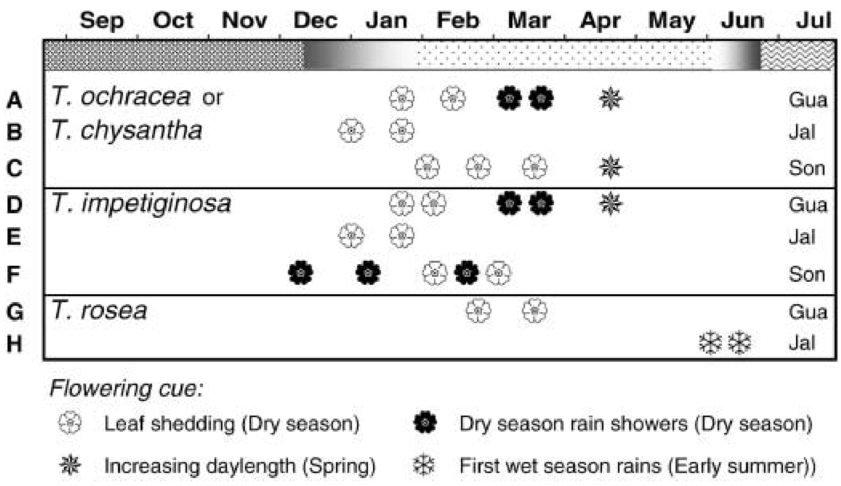

Figure 5 Phenotypic variation of flowering times observed in four species of *Tabebuia* in TDFs of Guanacaste (*Gua*), Jalisco (*Jal*) and Sonora (*Son*). Top: Vegetative phenology of *Tabebuia* represented as in Fig. 1d. Symbols indicate the flowering cue responsible for triggering anthesis at different times during the dry season (December–June).

Table 4 Fraction of species (% of all species in a TDF) and mean flowering times of flowering types in the TDFs of Guanacaste, Yucatan, Jalisco and Sonora. For definitions of flowering types see Table 1 and Methods

		Guanacaste		Yucatan		Jalisco		Sonora	
Flowering period	Flowering type	Species (%)	Flowering start (mo)	Species (%)	Flowering start (mo)	Species (%)	Flowering start (mo)	Species (%)	Flowering start (mo)
Wet season									
Foliated shoots	Summer	31	6.6 ± 0.8	37	6.0 ± 1.1	33	7.2 ± 0.6	15	7 ± 0.8
	Autumn	16	11.2 ± 1.3	10	11.4 ± 0.9	18	10.4 ± 0.9	8	10.6 ± 1.8
	Total†	47		47		51		23	
Leafless	Early summer					30	5.9 ± 0.5	3	6.5 ± 0.6
Dry season									
Foliated shoots	Winter	16	2.2 ± 1	15	3.1 ± 1.3	8	4.1 ± 1.9	10	2.7 ± 1.0
Leafless	Dry season	16	2 ± 1	27	2.8 ± 1.2	11	1.8 ± 0.9	18	1.0 ± 1.5
	Spring	20	4.2 ± 0.7	12	4.0 ± 0.8			45	4.8 ± 1.4
	Total‡	36		39		11		63	

†Total of autumn and Summer foliated shoots species; ‡total of Dry season and Spring Leafless species.

by genus and species. Flowering times varied widely among congeneric species in some genera, little in others. Congeneric species with low interspecific variation in flowering time were therefore included in the comparison of species-specific flowering times in the four forests (Fig. 4), but congeners with high variation were not.

The environmental controls indicated by arrows in Fig. 1 were deduced for each functional or flowering type from the temporal patterns of seasonal development (Introduction). Such all- or none responses of many conspecific trees to environmental cues require no statistical evaluation. In contrast, environmental controls of phenology cannot be deduced from community-wide means of flushing or flowering times (e.g. Frankie *et al.*, 1974; Bullock & Solis-Magallanes, 1990) and their correlations with environmental variables (Morellato *et al.*, 2000), because the temporal patterns of development characteristic of each functional and flowering type shown in Fig. 1 are lost when calculating community means.

RESULTS AND DISCUSSION

All flowering types established for the TDF of Guanacaste (Fig. 1f) are also found in the three Mexican TDFs (Fig. 3) and the means of flowering periods are similar for most, but not all flowering types (Table 4; Fig. 4). In each forest, flowering of some species is therefore likely to be caused by the combination of environmental cues and vegetative phenology defining each flowering type, but the fraction of species in the different flowering types varies widely among the four TDFs (Table 4; Fig. 3). An additional flowering type (Early summer species) was established for Jalisco and Sonora to define environmental flowering controls not observed in Guanacaste. The flowering periodicities represented by the different flowering types appear to be quite robust and the following analysis of the four sets of rather general phenological observations is well founded on our earlier, detailed phenological analyses (Rivera & Borchert, 2001; Borchert *et al.*, 2002; Rivera *et al.*, 2002). Nevertheless, our conclusions should be confirmed by detailed, high frequency phenological observations accompanied by recordings of precipitation and measurements of tree water status to identify flowering cues with greater confidence (Rivera *et al*., 2002; Borchert *et al*., 2002).

Flowering on foliated shoots

In Guanacaste, Yucatan and Jalisco, about half of the analysed species flower on foliated shoots during and soon after the 5–6 month-long wet season (Fig. 3a–c May/July–November; Table 4, Summer and Autumn species). About two thirds of these species flower during rain-induced shoot growth (Table 4, Summer species) and flowering of the remaining species is induced several months after the cessation of shoot growth by declining daylength (Table 4, Autumn species). An additional 22 species of shrubs in Guanacaste are Autumn species (Table 3). Autumn species flowering before the autumn equinox (August–September) are found only in the dry forests of Jalisco and Sonora (Fig. 4, Autumn species), where a physiologically significant reduction in daylength occurs sooner after the summer solstice than at the lower latitude of Guanacaste (Rivera & Borchert, 2001). Mean flowering start of Autumn species is therefore about one month later in Guanacaste than in these Mexican forests (Table 4; Fig. 4, Autumn species). In contrast, flowering periods among trees of several wide-ranging species are remarkably similar in the four forests (Fig. 4, Autumn species, Nov/Dec). In Sonora, where most nonriparian species flush during the summer rains, only a quarter of all species flower during or soon after shoot growth (Table 4, Summer and Autumn species; Fig. 3d).

In the TDFs of Guanacaste and Yucatan the fraction of species flowering during the dry season on the foliated shoots of leaf exchanging species is relatively large in comparison to the much drier forests of Jalisco and Sonora (Table 4, Fig. 3, Winter species). In addition, the majority of 93 shrub and treelet species in the semideciduous forest of Guanacaste flush and flower during the early dry season and hence are Winter species (Opler *et al*., 1980). The fraction of Winter species in a TDF thus appears to constitute a good indicator of the abundance of microsites with reliable, large subsoil water reserves, from which deep-rooted trees or shrubs can extract water during the dry season.

Dry season flowering on leafless branches

Episodes of shoot growth or flower expansion observed during the dry season in leafless trees of TDFs and other arid vegetation types indicate that trees have access to water needed for cell expansion in the growing organs. This requirement for water may be met by rain showers of > 20 mm, water absorption from subsoil water reserves by deep roots, or water storage in succulent tree stems or roots (Borchert, 1994a,b; Borchert *et al*., 2002). The following analysis is based on these observations.

In Guanacaste and Yucatan more than one third of the analysed tree species flower during the dry season between December and May on leafless shoots, only 11% do so in Jalisco, but two thirds of all species flower during this period in Sonora (Table 4, Dry season and Spring species; Fig. 3d, Jan–May). Water availability for flower development during seasonal drought thus varies widely among the four TDFs. In view of the similar seasonal rainfall distribution in Sonora and Jalisco (Fig. 2d,e), the prevalence of dry season flowering in Sonora raises the crucial question, why most Sonoran trees flower between March and June but only few do so in Jalisco (Fig. 3c,d).

In Guanacaste, similar numbers of species flower soon after leaf shedding during the early dry season and during the late dry season after the spring equinox (Table 4, Fig. 3a Dry season vs. Spring species). This indicates that dry-season flowering is induced either by leaf shedding (Dry season species) or by increasing daylength (Spring species), and flowering deciduous hardwood trees have access to subsoil water reserves throughout the dry season (Rivera *et al*., 2002). In the Yucatan TDF irregular rain showers during the dry season may provide up to 30% of annual precipitation and the dry season is therefore much less severe than in Guanacaste (Fig. 2b,c Dec–Mar). This affects flowering periodicity in two ways. First, the fraction of Dry season species with rain-induced flowering of leafless trees is by far the highest among the four analysed TDFs (Table 4, Dry season species). Second, dry season rain showers delay shedding of old leaves, a prerequisite for leaf-exchange and dry-season flowering of leafless trees (Borchert *et al*., 2002). Winter and Dry season species flower therefore about 1 month later than in Guanacaste (Table 4, Fig. 4, Winter and Dry season species).

In Jalisco, flowering induced by leaf shedding ends in January and very few species flower between February and May (Fig. 3c, Table 4, Winter and Dry season species), but the first summer rains in June/July trigger flowering on leafless shoots in many species (Fig. 3c, Table 4, Early summer species). These Early summer species include stem succulents (*Bursera*, *Plumeria*) as well as leaf-exchanging (*Thouinidium decandrum*), deciduous (*Caesalpinia eriostachys*, *Tabebuia chrysantha*, *T. rosea*) and spring-flushing hardwood species (*Bernardia*, *Casearia*, *Maclura*, *Prockia*, *Randia*), which in Guanacaste flower between January and April (Fig. 4, Winter, Dry season and Spring species; Frankie *et al*., 1974; Opler *et al*., 1980; Rivera *et al*., 2002). For example, in Guanacaste and Yucatan, *T. rosea* flowers soon after leaf shedding in February/March, but in Jalisco anthesis is delayed until after the first summer rains (Fig. 5g,h). The late flowering of these species in Jalisco indicates that soil water reserves have become depleted by February and severe drought prevents flower expansion before the first summer rains. This interpretation is supported by the observations that leaf fall is normally complete by late December (Maass *et al*., 1995) and an exceptionally early rainfall of 150 mm in May 1983 induced earlier than normal flowering in many species, including those mentioned above (Bullock, 1986a). In Guanacaste and Sonora, dry season flowering induced by leaf shedding (Dry season species) and increasing daylength (Spring species) are well separated in time from each other and from flowering on rain-induced new shoots (Summer species; Figs 3a,d and 5a,d), but in Jalisco flowering periods of these flowering types are merged with those of Early summer species because of the severe drought (Fig. 3c, Early summer species). Consequently, 80% of tree species in Jalisco flower during and soon after the wet season (Fig. 3c, Table 4, Early summer, Summer and Autumn species). The flowering periodicity of TDF trees indicates that in spite of a similar rainfall distribution, tree water stress during the dry season is greater in Jalisco than in Sonora, where lower winter temperatures and the resulting lower evaporation probably mitigate seasonal drought and soil water reserves appear to be larger (Fig. 2d,e).

Almost half the Sonoran tree species flower between March and early June, often 5–8 months after the last substantial rainfall and well before leaf flushing after the first summer rains in late June (Figs 2e, 3d and 4, Table 4, Spring flowering species). These spring-flowering species are in part hardwood trees, in part stem-succulent trees or arborescent cacti (Appendix, Spring and Succulent spring species). In the latter, water stored in succulent stems is available for flower expansion throughout the dry season (Borchert & Rivera, 2001), but the source of water available for flower expansion of hardwood trees remains to be identified. The distribution of Sonoran spring-flowering hardwood species provides a cue. Nine of 16 Spring species are found not only in the TDF, but also in the contiguous thornscrub receiving much lower precipitation (Appendix, Spring species). In this extremely dry habitat, trees are commonly confined to microsites such as arroyos (washes), where runoff from nearby slopes increases subsoil water storage to a level well above that provided by rainfall at the trees' location. *Prosopis* and other desert phreatophytes with deep root systems are well known to rely on such subsoil water reserves (Smith *et al*., 1997) and the same is probably true for TDF trees growing at the lower end of slopes or in arroyos. As in Guanacaste (Borchert, 1994a; Borchert *et al*., 2002), access to subsoil water reserves must constitute the prerequisite for the extensive spring flowering of leafless Sonoran hardwood trees, but it is hard to envisage the soil water reservoirs available to the many flowering TDF trees growing on rocky slopes with rather shallow soil. Studies of root systems and measurements of tree water status during the dry season are needed to verify the above interpretations.

Subsoil water reserves enabling spring flowering of Sonoran trees are replenished mainly during the summer rains and hence persist throughout the dry season. This raises the question why most deciduous trees do not use these water reserves to expand flowers before March. The regular mass flowering of species such as *Ipomoea arborescens*, *T. impetiginosa* and *Pachycereus pectin-aboriginum* between November and February indicates that the winter temperatures of southern Sonora do not inhibit flower development (Figs 2e and 3d). In all four TDFs, heavy rain showers between December and February induce leaf expansion in leafless trees of many species (Maas *et al*., 1995; Borchert *et al*., 2002; Bullock, 2003; Porter-Bolland, 2003; R.S. Felger, S. Meyer, pers. obs.) and mass flowering of Dry season species such as *T. impetiginosa* (Fig. 5) (Reich & Borchert, 1982; R.S. Felger, S. Meyer, pers. obs.). However, flowering soon after the relatively common winter rains (Fig. 2e) has not been observed in any Sonoran Spring species. Thus, flower buds of leafless Spring species trees are apparently dormant between the winter solstice and spring equinox, as also observed in spring flowering hardwood and stem succulent species in Guanacaste, Jalisco and elsewhere (Fig. 1b,c) (Bullock & Solis-Magallanes, 1990; Borchert & Rivera, 2001; Rivera *et al*., 2002). The synchronous mass flowering regularly observed in many species after the spring equinox (Figs 5a,d and 6a, March–June) (Van Devender *et al.,* 2000; Felger *et al*., 2001) therefore indicates that increasing daylength breaks the dormancy of flower buds and thus induces spring flowering episodes at the height of the dry season (Fig. 1f Spring) (Borchert & Rivera, 2001; Rivera *et al*., 2002). In Guanacaste, and probably in Yucatan, increasing daylength also induces the establishment of a full crown of leaves in many spring flushing species growing at moist sites (Fig. 1b) (Rivera *et al*., 2002), but in Sonora only partial leaf expansion before the summer rains has been observed in a few stem succulent (*Ceiba*, *Ipomoea*) and leguminous species (*Brongniartia*, *Lysiloma divaricata*, *Senna*; S. Meyer, pers. obs.). However, in many stem succulent species of the TDFs in Jalisco and Sonora, increasing daylength induces partial expansion of vegetative buds before the onset of rains, which enables preformed leaves to expand within one week after the first substantial summer rainfall (Gentry, 1942; Bullock & Solis-Magallanes, 1990; S. Meyer, pers. obs.). These observations indicate that soil water reserves in the Sonoran TDF are sufficient to support, in

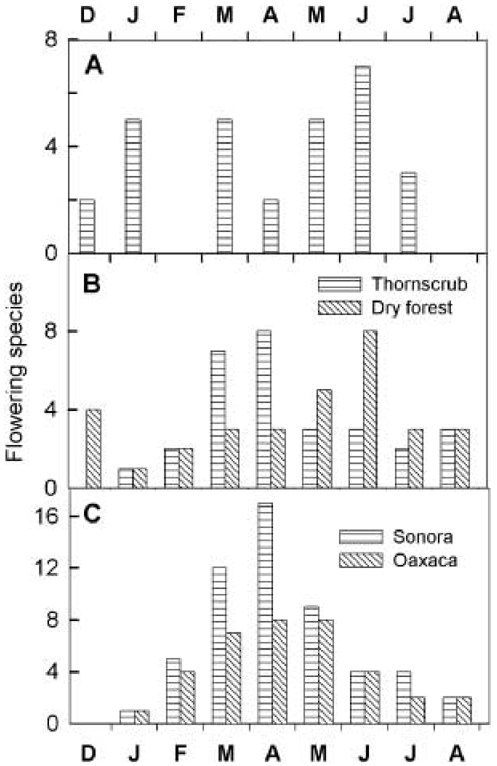

Figure 6 Flowering periodicity of different subpopulations of woody and succulent plants in Sonora, Mexico. (A) Beginning of mass flowering in the Sonora TDF. (B) Flowering periodicity in Sonoran desert- and thornscrub vs. tropical dry forest. (C) Flowering periodicity of cacti in Sonora and Central Mexico (Oaxaca). (Data for A, B from Appendix, cols. (g,h); data for C from Valiente-Banuet *et al*., 1996 and Paredes-Aguilar *et al*., 2000).

many species, flower expansion, but not shoot growth and leaf expansion.

Whereas mean flowering times induced by increasing daylength are similar in all TDFs (Table 4, Fig. 4 Spring species, Apr/May), the mean flowering times of leafless trees induced by rehydration after leaf shedding varies widely among the four TDFs, i.e. the phenotypic plasticity of flowering patterns is large. Leaf fall and subsequent flowering are induced earliest in Guanacaste and Sonora by early cessation of rainfall (Fig. 4, Dry season species, Nov–Dec) and later in Yucatan, where dry season rain showers delay leaf abscission (Fig. 4, Dry season species, Mar). In Jalisco, anthesis after early leaf shedding is in many species delayed by severe drought (Fig. 4, Early summer species, June–July). In Guanacaste and Sonora many wide-ranging species therefore flower 2–5 months before rain-induced flowering of their con-specifics in Jalisco (Fig. 4, Dry season and Spring species). This phenotypic plasticity of flowering patterns caused by variation in rainfall periodicity and soil water reserves is best documented for *Tabebuia*, a large, wide-ranging genus of deciduous TDF species, in which conspicuous trumpet-shaped flowers develop from resting terminal flower buds at various times after leaf abscission. Some trees display 2 or 3 flowering episodes during the same dry season, because partial flowering may be induced by leaf shedding soon after the last rains, isolated rain showers during the dry season, increasing daylength after the spring equinox or the first heavy rains of the wet season (Fig. 5) (Opler *et al.*, 1976; Reich & Borchert, 1982; Borchert, 1983, 1986; Bullock & Solis-Magallanes, 1990; Felger *et al.*, 2001; Rivera *et al.*, 2002; Porter-Bolland, 2003; S. Meyer, pers. obs.).

Proximate and ultimate causes of flowering periodicity

The analysis of the distribution of different flowering types among the four analysed TDFs strongly suggests that, like vegetative phenology, flowering periodicity at the species and community level is determined mainly by the periodicity of rainfall and soil water availability. Flowering periodicity is lowest in the evergreen rainforest of La Selva (Fig. 2a) and increases with increasing deciduousness caused by prolonged seasonal drought (Figs 2b,c and 3a,b). Flowering periodicity is most pronounced in the two Mexican TDFs with the lowest annual rainfall and similar rainfall periodicity (Figs 2d,e and 3c,d), which represent alternate patterns of environmental control of flowering. In the dry upland forest of Jalisco, dry season flowering remains suppressed by lack of adequate subsoil water reserves (Fig. 3c). In Sonora, most trees flower between March and mid-June, during the hottest and driest part of the year, but leaf flushing is confined to the short summer growing season (Fig. 3d). Spring flowering during March–May is even more pronounced among Sonoran thornscrub species and cacti adapted to arid habitats (Fig. 6b,c). In analogous fashion to photoperiodic control of bud dormancy in cold-temperate trees, declining photoperiod in autumn induces dormancy of flower buds in spring flowering species and increasing daylength after the spring equinox triggers bud break and mass flowering (Rivera *et al.*, 2002). Like other unique structural and functional adaptations of woody plants to arid habitats (Smith *et al.*, 1997), the temporal separation of shoot growth and flowering observed in most Sonoran TDF trees, as well as in several desert tree species (Bowers & Dimmit, 1994), apparently constitutes an important adaptation of tree development to a strongly seasonal, semiarid climate, where optimization of vegetative development during the short growing season may be crucial for tree survival.

Climatic periodicity thus constitutes both the proximate and the principal ultimate cause of spring flowering and summer flushing at the species and community level. Implicitly, it appears unlikely that the characteristic flowering periodicity of Sonoran trees, in particular, and dry season flowering of tropical deciduous trees, in general, should have evolved in response to interactions with animal pollinators or seed dispersers (Janzen, 1967; Wright, 1996). Both native stingless bees (*Melipona beechei*) and introduced honeybees visit all the tree species of the Yucatan TDF analysed here in an opportunistic manner (Porter-Bolland, 2003). For such generalist pollinators, interannual variation in flowering patterns of individual tree species and the large phenotypic plasticity of flowering phenology observed in many TDF species do not matter, because they rely on the entire set of acceptable tree species (Bronstein, 1995; Porter-Bolland, 2003). Thus, there appears to be no ecological base for the postulated adaptation of flowering time to pollinator availability (Wright, 1996) and except for a few highly specialized mutualistic systems (see below) there is no evidence for a crucial role of flowering time in plant–pollinator interaction (Bronstein, 1995).

Photoperiodic control of spring flowering constitutes a unique timing mechanism enabling synchronous mass flowering and the selection of species or ecotypes with staggered flowering periods, which are crucial elements in the strong interdependence between arborescent cacti and their animal pollinators (Thomas & Vince-Prue, 1997; Fleming, 2000). Most cacti of Sonora and Central Mexico flower synchronously for 1–2 months between March and May (Fig. 6c, Appendix, Succulent spring species; Valiente-Banuet *et al.*, 1996; Fleming, 2000; Paredes-Aguilar *et al.*, 2000). As in stem-succulent trees synchronous spring flowering of cacti must be induced by increasing daylength (Rivera *et al.*, 2002). Given the patchiness and large year-to-year variation of rainfall in the arid habitats of cacti, photoperiodic control constitutes the only proximate mechanism capable of inducing synchronous flowering of all cacti in a landscape at the same species-specific time each year (Rivera *et al.*, 2002). Synchronized flowering provides a large and reliable source of nectar and is a prerequisite for attracting the regular visits of pollinators to cacti, whose flowers remain open for only a few hours (Fleming, 2000).

ACKNOWLEDGEMENTS

We thank Dr Stephen Bullock, Ensenada, Mexico, Zoraida Calle, Cali, Colombia, and an anonymous reviewer for helpful and critical comments on the manuscript.

REFERENCES

Borchert, R. (1983) Phenology and control of flowering in tropical trees. *Biotropica*, **15**, 81–89.

Borchert, R. (1986) *Tabebuia* (trumpet tree). *CRC Handbook of flowering*, Vol. V (ed. by A.H. Halevy), pp. 345–352. CRC Press, Boca Raton, FL.

Borchert, R. (1994a) Water storage in soil or tree stems determines phenology and distribution of tropical dry forest trees. *Ecology*, **75**, 1437–1449.

Borchert, R. (1994b) Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees*, **8**, 198–204.

Borchert, R. (2000) Organismic and environmental controls of bud growth in tropical trees. *Dormancy in plants: from whole plant behaviour to cellular control* (ed. by J.D. Viemont and J. Crabbe), pp. 87–107. CAB International, Wallingford, UK.

Borchert, R. (2003) Environmental control of vegetative phenology in tropical dry forest trees. *Physiological plant ecology* (W. Larcher), pp. 337–340. Springer, Berlin.

Borchert, R. & Rivera, G. (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiology*, **21**, 213–221.

Borchert, R., Rivera, G. & Hagnauer, W. (2002) Modification of vegetative phenology in a tropical semideciduous forest by abnormal drought and rain. *Biotropica*, **34**, 27–39.

Bowers, J.E. & Dimmitt, M.A. (1994) Flowering phenology of six woody plants in the northern Sonoran Desert. *Bulletin of the Torrey Botanical Club*, **121**, 215–229.

Bronstein, J.L. (1995) The plant-pollinator landscape. *Mosaic landscapes and ecological processes* (ed. by L. Hanson, I. Fahrig and G. Merriam), pp. 257–288. Chapman & Hall, London.

Bullock, S.H. (1986a) Observations and an experiment on synchronous flowering. *Madroño*, **33**, 223–224.

Bullock, S.H. (1986b) Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Archives for Meteorology, Geophysics and Bioclimatology. Series B*, **36**, 297–316.

Bullock, S.H. (1995) Plant reproduction in neotropical forests. *Seasonally dry tropical forests* (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 277–303. Cambridge University Press, Cambridge.

Bullock, S.H. (2003) La fenologìa de plantas en Chamela. *Historia natural de chamela* (ed. by F.A. Noguera, J.H. Vega Rivera, A.N. Garcia Aldrete and M. Quesada Avendaño), pp. 491–498. Instituto de Biologìa, Universidad Autónoma de Mexico, Mexico City.

Bullock, S.H. & Solis-Magallanes, J.A. (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica*, **22**, 22–35.

Felger, R.S., Johnson, M.B. & Wilson, M.F. (2001) *The trees of Sonora, Mexico*. Oxford University Press, Oxford.

Fleming, T.H. (2000) Pollination of cacti in the Sonoran desert. *American Scientist*, **88**, 432–439.

Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881–919.

Gentry, H.S. (1942) *Rio Mayo plants*. Carnegie Institution of Washington, Washington D.C. Publication 527.

Janzen, D. (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, **21**, 620–637.

Maass, J.M., Vose, J.M., Swank, W.T. & Martinez-Yrizar, A. (1995) Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management*, **74**, 71–180.

Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C. & Ziparro, V.B. (2000) Phenology of Atlantic rain forest trees, a comparative study. *Biotropica*, **32**, 811–823.

Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications*, **5**, 363–385.

Opler, P.A., Frankie, G.W. & Baker, H.G. (1976) Rainfall as a factor in the release, timing and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography*, **3**, 321–326.

Opler, P.A., Frankie, G.W. & Baker, H.G. (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **68**, 167–188.

Paredes-Aguilar, R., Van Devender, T.R. & Felger, R.S. (2000) *Cactaceas de Sonora, Mexico, su diversidad, uso y conservación*. Arizona-Sonora Desert Museum, Tucson.

Porter-Bolland, L. (2003) La apicultura y el paisaje maya. Estudio sobre la fenología de floración de las especies melíferas y su relación con el ciclo apícola en La Montaña, Campeche, México. *Mexican Studies/ Estudios Mexicanos*, **19**, 303–330.

Reich, P.B. & Borchert, R. (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology*, **63**, 294–299.

Rivera, G. & Borchert, R. (2001) Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium specimens. *Tree Physiology*, **21**, 201–212.

Rivera, G., Elliott, S., Caldas, L.S., Nicolossi, G., Coradin, V.T.R. & Borchert, R. (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees*, **16**, 445–456.

Robichaux, R.H. & Yetman, D.A. (2000) *The tropical deciduous forest of Alamos. Biodiversity of a threatened ecosystem in Mexico*. University of Arizona Press, Tucson.

Smith, S.D., Monson, R.K. & Anderson, J.E. (1997) *Physiological ecology of North American desert plants*. Springer Verlag, Berlin.

Thomas, B. & Vince-Prue, D. (1997) *Photoperiodism in plants*. Academic Press, San Diego.

Valiente-Banuet, A., Arizmendi, M., Rojas-Martinez, A. & Dominguez-Canseco, L. (1995) Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology*, **12**, 103–119.

Van Devender, T., Sanders, A.C., Wilson, R.K. & Meyer, S.A. (2000) Vegetation, flora and seasons of the Rio Cuchujaqui, a tropical deciduous forest near Alamos, Sonora. *The tropical deciduous forest of Alamos* (ed. by R.H. Robichaux & D.A. Yetman), pp. 36–101. The University of Arizona Press, Tucson.

Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, London.

Wright, S.J. (1996) Phenological responses to seasonality in tropical forest plants. *Tropical forest ecophysiology* (ed. by S.D. Mulkey, R.L. Chazdon and A.P. Smith), pp. 440–460. Chapman & Hall, New York.

WWF (2001) [Central America]; nt119 [Costa Rica]; nt 230 [Southern Pacific Mexico]; nt228 [Sinaloa]; na0201 [Sonora]. [WWW document]. URL http://www.worldwildlife.org/wildworld/profiles/terrestrial/nt/ nt0209_full.html#location

BIOSKETCHES

Rolf Borchert is Professor Emeritus of Ecophysiology in the Division of Biological Sciences, University of Kansas, Lawrence, KS, USA. He has analysed the environmental control of the phenology of tropical forest trees for more than 25 years.

Stefanie Meyer is a nature guide in Alamos, Sonora, Mexico.

Richard Felger is Director of the Dryland Institute in Tucson, Arizona, USA. He has studied the plant life, ethnobiology, and conservation of the Sonoran Desert region for more than 30 years. He coauthored *The Trees of Sonora*, *Mexcio* and several other books.

Luciana Porter-Bolland is a researcher at the Instituto de Ecologia in Xalapa, Mexcico. She studied the phenology of honey-producing trees in the central Yucatan peninsula for her doctoral thesis at the University of Florida.

Appendix Tree species of Sonora (Felger *et al*., 2001) sorted by flowering type and first month of flowering. Authorities for scientific names and full family names are given in Felger *et al*. (2001). Flowering period: x, normal flowering; X, mass flowering; stippling, main rainy season. Columns A–I: A, Flowering type (Su–Summer species; Au–Autumn species; Wi–Winter species; Ds–Dry season species; Sp–Spring species; Sc–Succulent spring species; Es–Early summer species). B, First month of flowering; C, Duration of flowering (months); D, Mass flowering (month); E, Leaf phenology (1, early drought-deciduous; 2, drought-deciduous; 3, late drought-deciduous; 4, leaf-exchanging; 5, evergreen). F, Soil or stem water availability (1, species not restricted to moist sites; 2, arroyo or riparian species; 3, stem succulent). G–I Habitats (G, tropical dry forest; H, thornscrub; I, desertscrub).

		Flowering period (calendar month)												**Flowering**				**Leaves**		**Habitat**		
Species		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**
Esenbeckia hartmannii	Ruta						x	X	x					**Su**	6	3	7	3	1	x	x	x
Sideroxylon tepicense	Sapo							x	x					**Su**	7	2	6	3	1	x		
Hintonia latifolia	Rubi							X	X	x				**Su**	7	3	7	2	1	x	x	x
Jatropha cordata	Euph							x	x					**Su**	7	2		2	1	x	x	x
Lysiloma divaricatum	Mimo							x	x	x		x		**Su**	7	5		2	2	x	x	x
Maclura tinctoria	Mora							x	x	x				**Su**	7	3		2	2	x		
Mimosa palmeri	Mimo							x	x	x				**Su**	7	4		2	1	x	x	
Wimmeria mexicana	Cela							X	X	x				**Su**	7	3	7	3	1	x		
Ziziphys amole	Rham							x	x	x				**Su**	7	3		2	1	x	x	x
Bursera hindsiana	Burs								x	x				**Su**	8	3		1	3			x
Caesalpinia sclerocarpa	Caes								x	x				**Su**	8	2		2	2		x	
Fouquieria columnaris	Fouq								x	x				**Su**	8	2		2	3			x
Leucaena lanceolata	Mimo								x	x				**Su**	8	2		2	1	x	x	
Thouinia acuminata	Sapi								x	x				**Su**	8	2			2	x		
Trichilia americana	Meli								x	x				**Su**	8	2		3	2	x		
Heliocarpus attenuatus	Tili								x	x				**Su**	8	3		2	1	x	x	x
Heliocarpus palmeri	Tili								x	x				**Au**	8	3		2	2	x		
Alvaradoa amorphoides	Sima									x				**Au**	9	2			1	x	x	
Citharexylum scabrum	Verb									x				**Au**	9	1			1	x	x	
Psidium sartorianum	Myrt											x		**Au**	10	3		5	2	x		
Acacia farnesiana	Mimo	x	x	x	x							x	x	**Au**	11	6		3	1	x	x	x
Sapindus saponaria	Sapi	x	x									x	x	**Au**	11	4		2	2	x	x	x
Sideroxylon persimile	Sapo	x										x	x	**Au**	11	3		3	2	x		
Trophis racemosa	Mora											x	x	**Au**	11	2		5	2	x		
Agonandra racemosa	Opil	x	x	x	x	x							x	**Au**	12	6			2	x	x	
Cochlospermum vitifolium	Coch	X	X	x									x	**Au**	12	4	1	2	2	x		
Montanoa tomentosa	Aste	x	x										x	**Au**	12	3		2	1	x		
Cordia sonorae	Bora	x		X	X	X								**Au**	1	4	3	3	2	x	x	x
Pachycereus pecten-aboriginum	Cact	x	x	x										**Au**	1	3		—	3	x	x	
Pithecellobium dulce	Mimo	x	x	x									x	**Wi**	12	4		?	2	x	x	
Populus mexicana	Sali	x	x											**Wi**	1	2		4	2	x	x	
Amyris balsamifera	Ruta		x	x										**Wi**	2	2		4–5	2		x	x
Thouinia villosa	Sapi		x	x		x								**Wi**	2	3			2	x		
Celtis iguanea	Ulma			x	x	x	x	x						**Wi**	3	5		4	2	x	x	
Celtis reticulata	Ulma			x	x	x	x							**Wi**	3	4		4, 6	2	x	x	x
Forchhammeria watsonii	Capp			X	X									**Wi**	3	2	3	4	2		x	x
Harvardia mexicana	Mimo			x	x	x								**Wi**	3	3			2	x	x	x
Lysiloma candidum	Mimo			x	x	x								**Wi**	3	3		6	2			x
Vitex mollis	Verb			x	x	x								**Wi**	3	3		5	2	x	x	
Lysiloma watsonii	Mimo				x	x								**Wi**	4	2		5	2	x	x	
Melia azedarach	Meli				x	x								**Wi**	4	2		6	2	x		
Croton fantzianus	Euph	x	x	x								x	X	**Ds**	11	5	12	2	1	x		
Ipomoea arborescens	Conv	X	x	x								x	X	**Ds**	11	5	12	2	3	x	x	x
Tabebuia impetigunosa	Bign	X	X	X	x							x	X	**Ds**	11	6	1	2	2	x	x	
Bauhinia pringlei	Caes	X	X	x									x	**Ds**	12	4	1	2	1	x		
Caesalpinia caladenia	Caes	x	x	x									x	**Ds**	12	4		2	1	x	x	

		Flowering period (calendar month)												**Flowering**				**Leaves**		**Habitat**		
Species		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**
Schoepfia schreberi	Olac	x	x	x									x	**Ds**	12	4		2	2	x		
Coursetia glandulosa	Faba	X	X	X	X									**Ds**	1	4	1	3	1	x	x	x
Pisonia capitata	Nyct	x	x	x	x									**Ds**	1	4		3	2	x	x	
Tabebuia chrysantha	Bign	x	x	x			x							**Ds**	1	3		2	1	x		
Acacia occidentalis	Mimo		x	x	x									**Ds**	2	3		3	1	x	x	x
Parkinsonia florida	Caes		x	x	x	x								**Ds**	2	4		2	1		x	x
Pseudobombax palmeri	Bomb		x	x	x									**Ds**	2	3		1	3	x		
Caesalpinia palmeri	Caes			X	X									**Ds**	3	2	3	2	1		x	x
Diphysa suberosa	Faba			x	x	x	x	x						**Ds**	3	5		2	1	x	x	x
Platymiscium trifoliolatum	Faba			x	x									**Ds**	3	2		3	2	x		
Spondias purpurea	Anac			x	x									**Ds**	3	2		1	3	x		
Crateva palmeri	Capp			x	x									**Sp**	3	2		2	2	x	x	
Parkinsonia microphylla	Caes			X	X	X								**Sp**	3	3	3	2	1			x
Prosopis velutina	Mimo			x	x	x								**Sp**	3	3		2	2		x	x
Senna atomaria	Caes			x	X	x	x							**Sp**	3	5		2	1	x	x	
Capparis atamisquea	Capp				x	x	x							**Sp**	4	3		5	2			x
Castela emoryi	Sima				x	x	x							**Sp**	4	3		2	1			x
Eysenhardtia orthocarpa	Faba				x	x	x	x	x	x				**Sp**	4	6		3	1	x	x	x
Cephalanthus salicifolius	Rubi				x	x	x	x	x	x				**Sp**	4	6		6	2	x	x	
Olneya tesota	Faba				X	X								**Sp**	4	2	4	3	1		x	x
Parkinsonia aculeata	Caes				X									**Sp**	4	1	4	1	1	x	x	x
Prosopis articulata	Mimo				x	x								**Sp**	4	2		2	1		x	x
Prosopis glandulosa	Mimo				x	x	x							**Sp**	4	3		2	1	x	x	x
Vitex pyramidata	Verb				x	x	x	x	x					**Sp**	4	5		5	1	x		
Aphananthe monoica	Ulma					x	x	x						**Sp**	5	3		5	2	x		
Albizia sinaloensis	Mimo					x								**Sp**	5	1		3	2	x	x	
Brongniartia alamosana	Faba					X	X	x						**Sp**	5	3	5	2	2	x	x	
Canotia holocantha	Cela					x	x							**Sp**	5	2			1			x
Diospyros sonorae	Eben					x	x							**Sp**	5	2		5	2	x	x	
Erythroxylum mexicanum	Eryt					x	x							**Sp**	5	2		3	1	x		
Guajacum coulteri	Zygo					X	x	x						**Sp**	5	3	5	5	1	x	x	x
Guazuma ulmifolia	Ster					x	x	x	x	x				**Sp**	5	5		3	2	x	x	x
Lonchocarpus hermannii	Faba					X	X							**Sp**	5	2	5	2	1	x		
Prosopis pubescens	Mimo					x								**Sp**	5	1		2	2			x
Psidium guajava	Myrt					x	x							**Sp**	5	2		5	2	x		
Trichilia hirta	Meli					x	x	x	x					**Sp**	5	4		3	2	x		
Vauquelinia californica	Rosa					x	x	x	x					**Sp**	5	4		5	2			x
Capparis flexuosa	Capp						x	x						**Sp**	6	2		5	2		x	
Chloroleucon mangense	Mimo						X	x						**Sp**	6	3	6	2	1	x		
Coccoloba goldmanii	Poly						x	x						**Sp**	6	2		5	2	x	x	x
Harvardia sonorae	Mimo						x	x	x					**Sp**	6	3			2		x	x
Conzattia multiflora	Caes						x	x						**Sp**	6	2		1	1	x		
Karwinskia humboldtiana	Rham						x	x						**Sp**	6			3	1	x	x	x
Piscidia mollis	Faba						X	X						**Sp**	6	2	6	2	2	x	x	
Psorothamnus spinosus	Faba						X	X						**Sp**	6	2	6	1	1			x
Randia echinocarpa	Rubi						x	x						**Sp**	6	2		2	1	x	x	
Randia laevigata	Rubi						x							**Sp**	6	1		2	1	x	x	
Randia obcordata	Rubi						x	x						**Sp**	6	2		2	1	x	x	x
Sebastiania pavoniana	Euph						x	x	x					**Sp**	6	3		3	2	x		
Colubrina triflora	Rham						x	x	x	x				**Sp**	8	4		3	2	x		
Crescentia alata	Bign			x	x	x	x							**Sc**	3	4		5	3	x		
Opuntia thurberi	Cact			x	x	x								**Sc**	3	3		—	3	x	x	
Opuntia versicolor	Cact			x	x	x								**Sc**	3	3		—	3		x	x
Pachycereus pringlei	Cact			x	x	x								**Sc**	3	3		—	3			x
Vallesia lacinata	Apoc			X	X	X								**Sc**	3	3	3		3		x	x
Carnegia gigantea	Cact				x	x								**Sc**	4	2		—	3		x	x

Species		Flowering period (calendar month)												Flowering				Leaves		Habitat		
		1	2	3	4	5	6	7	8	9	10	11	12	A	B	C	D	E	F	G	H	I
Lophocereus schottii	Cact				x	x	x	x	x	x				**Sc**	4	6		—	3			x
Opuntia fulgida	Cact				x	x								**Sc**	4	2		—	3			x
Opuntia wlcoxii	Cact				x	x								**Sc**	4	2		—	3	x	x	
Stenocereus montanus	Cact				x	x								**Sc**	4	2		—	3	x		
Ceiba acuminata	Bomb					x	X			x				**Sc**	5	3	6	1	3	x	x	
Erythrina flabelliformis	Faba					X	X	x						**Sc**	5	3	5	1	1	x	x	x
Jatropha malacophylla	Euph					X	X							**Sc**	5	2	4	2	3	x		
Plumeria rubra	Apoc					X	X	x						**Sc**	5	3	5	1	3	x	x	x
Stemmadenia tomentosa	Apoc					x	x	x	x					**Sc**	5	4		1	3	x		
Bursera grandifolia	Burs						X							**Sc**	6	1	6	1	3	x		
Bursera lancifolia	Burs						X	x						**Sc**	6	2	6	1	3	x	x	
Bursera laxiflora	Burs						X	x	x					**Sc**	6	3	6	1	3	x	x	x
Bursera simarouba	Burs						x	x						**Sc**	6	2		1	3	x		
Pilosocereus alensis	Cact						x							**Sc**	6	1		—	3	x		
Bursera fagaroides	Burs						x	x						**Es**	6	2		1	3	x	x	x
Bursera stenophylla	Burs						x	x						**Es**	6	2		1	3	x		
Bursera microphylla	Burs							x						**Es**	7	1		1	3			x
Bursera penicillata	Burs							x	x					**Es**	7	2		1	3	x		