

FACTORS AFFECTING PHENOLOGICAL PATTERNS OF BOMBACACEOUS TREES IN SEASONAL FORESTS IN COSTA RICA AND MEXICO¹

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We compared phenological patterns of tree species of the family Bombacaceae in three seasonal forests in Mexico and Costa Rica whose dry seasons vary in duration and intensity. The objectives were to (1) determine intraspecific variation in phenology between sites in different geographic locations with different precipitation regimes, (2) compare interspecific phenological patterns within sites during one year, and (3) document seasonal pollinator use of floral resources at one site in relation to the flowering phenology of these species. To determine the sequence of phenological events in trees of the family Bombacaceae across three study sites, phenology of marked individuals was recorded every 2 wk from September 2000 through August 2001 for six species. To estimate the importance of bombacaceous species in the diet of nectarivorous bats, pollen samples were collected from the bodies or feces of bats once every 2 wk during flowering. Our study suggests that phenological patterns of the Bombacaceae family in Neotropical dry forests are mainly constrained by phylogenetic membership and adaptive selective pressures associated with competition for pollinators. Abiotic factors related to precipitation and soil water content appear to be regulating leaf flushing and abscission, but the principal causes of flowering are related to ultimate factors associated with competition for pollinators. This study is the first that evaluates the phenological pattern of species and genera of the same family at different latitudes in a similar life zone.

Key words: Bombacaceae; Costa Rica; Mexico; nectarivorous bats; Neotropics; phenology; plant reproduction; pollinator competition.

Phenological events in plants may be affected by various factors that can be classified as proximate or ultimate causes. Proximate causes principally include short-term environmental events that may trigger phenological patterns, while ultimate causes include evolutionary forces that are responsible for these patterns. Environmental cues such as changes in water level stored by plants (Reich and Borchert, 1984; Borchert, 1994; but see Wright and Cornejo, 1990; Wright, 1991), seasonal variations in rainfall (Opler et al., 1976), changes in temperature (Ashton et al., 1988; Williams-Linera, 1997), photoperiod (Leopold, 1951; Tallak Nilsen and Huller, 1981; van Schaik, 1986; Rivera et al., 2002), irradiance (Wright and van Schaik, 1994), and sporadic climatic events (Sakai et al., 1999) have been mentioned as proximate causes triggering phenological events in tropical plants. In forests with a marked dry season, changes in water availability from shifts in precipitation regimes and soil moisture have been proposed as the es-

sential proximate and ultimate causes affecting phenological patterns (Reich and Borchert, 1984; Borchert, 1994).

In contrast, biotic factors, such as competition for pollinators or pollinator attraction (Robertson, 1895; Janzen, 1967; Gentry, 1974; Stiles, 1975; Augspurger, 1981; Appanah, 1985; Murray et al., 1987; Sakai et al., 1999), competition for seed dispersers (Snow, 1965), and avoidance of herbivory (Marquis, 1988; Aide, 1993; van Schaik et al., 1993; Coley and Barone, 1996) have been interpreted as ultimate causes responsible for phenological patterns in tropical species. Biotic factors have been suggested as affecting phenological synchronization between species within the same guild (Frankie et al., 1974; Stiles 1977).

Finally, some studies have suggested that plant phenology is principally constrained by phylogenetic membership or life form (Kochmer and Handel, 1986; Wright and Calderón, 1995). This hypothesis supports the idea that phylogenetic constraints are stronger than local selective pressure, thus members of the same taxa should have similar phenological patterns regardless of geographical location (Kochmer and Handel, 1986).

Few studies have evaluated proximate and ultimate causes of phenological patterns of plants in different environments or geographic regions and most of these studies compared communities (Frankie et al., 1974; van Schaik et al., 1993; Murali and Sukumar, 1994). Frankie et al. (1974) reported that greatest leaf fall corresponded to the driest periods both in wet (La Selva) and dry forests (Comelco) in Costa Rica. This study concluded that synchronization in flowering during particular seasons depended on climatic conditions. Nonetheless, they suggest that biotic factors, such as competition for pollinators, also may have a subtle but important influence on flowering

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phenology. Another study comparing two tropical dry forest sites with different annual rainfall in southern India concluded that phenological patterns depend upon precipitation (Murali and Sukumar, 1994). However, they recognized the importance of ultimate causes and suggested that in some species flowering phenology might be determined by competition for pollinators.

Comparative phenological studies of plants of the same taxa over different geographic locations that vary in climatic conditions or pollinator assemblages may help to establish the relative importance of different hypotheses to explain phenological patterns. These comparisons will determine if phenological variation is due to changes in climatic conditions between sites or are a response to biological factors such as competition for pollinators within sites. This study focuses on phenological patterns of tree species of the family Bombacaceae in three seasonal forests in Mexico and Costa Rica that vary in dry season duration and intensity. Our objectives include (1) determining intraspecific variation in phenology between sites in different geographic locations with different precipitation regimes, (2) comparing interspecific phenological patterns within sites during one year, and (3) documenting seasonal pollinator use of floral resources at one site in relation to the flowering phenology of these species.

If the intensity and duration of the dry season are the main factors affecting phenological patterns in the members of the family Bombacaceae, we expect to find significant differences in the onset of leaf flushing, flowering, and fruiting between sites within species. Conversely, if competition for pollinators is one of the most important factors in determining phenological events in the species studied, we expect to find a sequential pattern of peak flowering dates of each species within sites (i.e., staggered flowering). Furthermore, if competition for pollinators is affecting the phenological patterns of Bombacaceae, we expect that the species of pollinators will be using the same bombacaceous plants within sites and that they will sequentially concentrate on the different species of plants depending on their flowering pattern.

MATERIALS AND METHODS

Study sites—This study was conducted in three seasonal tropical forests on the Pacific coast of Mesoamerica, which differ in precipitation regime, average temperature, and dry season duration. The first site was located in the central Pacific coast of Mexico within and surrounding the Chamela-Cuixmala Biosphere Reserve (ca. 19°30' N, 105°03' W). This reserve is located approximately between Puerto Vallarta, Jalisco, and Manzanillo, Colima, and has an extension of 13 200 ha (Ceballos and García, 1995). The predominant vegetation type in this area is tropical dry forest. Average annual rainfall is 707 mm with a dry season from November through June. The majority of the tree species are deciduous, abscising their leaves during the dry season and producing flowers (Bullock and Solís-Magallanes, 1990). This site will be referred to hereafter as Chamela-Cuixmala.

The second site was located in the northern Pacific coast of Costa Rica in the province of Guanacaste (10°45' N, 85°30' W) within the Guanacaste Conservation Area. This protected area is considered tropical dry forest according to the life zone classification system proposed by Holdridge (1969). Average annual rainfall is 1440 mm, and the dry season extends from December through April (Maldonado et al., 1995). Most of the tree species are deciduous and their flowering peak occurs during the dry season (Frankie et al., 1974). This site will be referred to hereafter as Guanacaste.

The third site was located in the Osa Peninsula in the southern Pacific coast of Costa Rica (8°26' N, 83°30' W) within the Osa Conservation Area (ACOSA). This area is considered tropical moist forest according to Holdridge

(1969), and average annual rainfall is 3000 mm in the lowlands and 4000 mm in the uplands, with a marked dry season from December to April (Hartshorn, 1983). Most tree species are evergreen, and only a few drop their leaves during specific intervals of the dry season (December–March; Allen, 1956). This site will be referred to hereafter as Osa.

Study species—We studied six species from the family Bombacaceae at the three study sites. All species studied possess hermaphroditic, chiropterophilic flowers that are principally visited by bats and sphingid moths (Alvárez and González-Quintero, 1970; Heithaus et al., 1975; Quiroz et al., 1983; Eguiarte et al., 1987; Haber and Frankie, 1989; Stoner et al., 2002, 2003). All species are characterized by compound digitate leaves that abscise prior to flowering in the dry season and produce new leaves in the rainy season. With the exception of *C. aesculifolia*, all fruits mature during the dry season after flowering (Frankie et al., 1974; Bullock, 1995). Fruits are five-valved, woody, and dehiscent with abundant kapok fibers surrounding the seeds for wind dispersal (Cascante-Marín, 1997; Avendaño-Reyes, 1998).

Ceiba aesculifolia is a Neotropical species distributed from Mexico to northern Costa Rica (Avendaño-Reyes, 1998). Trees may grow up to 20 m in height and have diameters of 20–50 cm. *Ceiba aesculifolia* has large (10–16 cm) flowers with five brown pubescent petals and five white filaments with yellow stamens. Styles are on average 15 cm long and surpass the stamens by 1–2 cm. Very little information exists on the reproductive biology of this species.

Ceiba grandiflora has only been reported from the states of Jalisco and Colima, Mexico, and thus appears to be an endemic tree species to the tropical dry forest in this region (Rose, 1895; Lott, 1993). This is a relatively short species (<12 m) with a diameter up to 60 cm. The actinomorphic flowers are cream-colored with petals approximately 9–12 cm long with five stamens with cream-colored filaments united at the base (Rose, 1895).

Ceiba pentandra is distributed in the Neotropics from México to the Amazonian basin and in the paleotropics throughout western Africa (Hartshorn, 1983). This species is a tall (>40 m) emergent deciduous tree that may reach diameters (dbh) of more than 200 cm. Flowers are small (3–3.5 cm) with five stamens around a protruding style with white to pink petals (Cascante-Marín, 1997).

Pachira quinata is a Neotropical species distributed in dry forests from Honduras to northern South America (Alverson, 1994). Trees may grow up to 35 m in height with diameters (dbh) over 100 cm. Flowers are medium-sized (5–10 cm) and protandrous, with multistaminate white filaments and a single central style (Quesada et al., 2001; Fuchs et al., 2003).

Pseudobombax ellipticum is found only in Mexico along the Gulf of Mexico from Tamaulipas and San Luis Potosí to the Yucatan Peninsula and on the Pacific side from Sinaloa to Chiapas. This species is relatively short (<12 m) with a diameter up to 60 cm. Flowers are multistaminate and actinomorphic, 13–15 cm long with light pink coloration on the base of the petals (Pennington and Sarukhán, 1998).

Pseudobombax septenatum is distributed from Nicaragua to Brazil (Quesada et al., 1997). Trees are usually tall (>30 m), and the trunk has green, vertical stripes separated by grayish bark. The trunk varies in diameter according to water storage. Flowers are large (15–20 cm) with a single central style. Light pink flowers are multi-staminate with denser stamens and thicker filaments than in other genera.

Phenology data—To determine the sequence of phenological events in trees of the family Bombacaceae across the three study sites, we recorded the phenology of marked individuals every 2 wk from September 2000 through August 2001 for all six species. Individuals were marked along access roads and permanent trails within all three sites. We used 55 individuals of *Ceiba aesculifolia*, 83 individuals of *Ceiba grandiflora*, 21 individuals of *Ceiba pentandra*, and 34 individuals of *Pseudobombax ellipticum* in Chamela-Cuixmala. In Costa Rica, we determined the phenology of 33 individuals of *C. aesculifolia*, 35 of *C. pentandra*, 98 of *Pachira quinata*, and 20 of *Pseudobombax septenatum* in Guanacaste. In Osa, phenological data was collected for 67 individuals of *C. pentandra* and 72 of *Pseudobombax septenatum*. In total, phenology data was collected for 518 trees across all three sites.

TABLE 1. Climatic data from three seasonal forests studied in Mexico and Costa Rica for the years 2000–2002.

Site	Temperature ^a	Photoperiod (h)	Rainy season		Dry season	
			Duration	Precipitation ^b (mm)	Duration	Precipitation ^b (mm)
Chamela	29.3°–18.1°C	10.8–13.2	July–October	124	November–June ^c	6.9
Guanacaste	32.8°–21.8°C	11.4–12.6	May–November	175	December–April ^d	0.3
Osa	31.9°–21.8°C	11.4–12.6	April–November	383	December–March ^d	118.3

^a Average monthly values during respective season, maximum–minimum range.

^b Average monthly values during respective season.

^c Less than 50 mm of precipitation per month.

^d Less than 150 mm of precipitation per month.

We determined the phenology of all species for each sampling date by scoring leaf, flower, and fruit production. Quantitative estimation of leaf production was not possible, but the dates of leaf flush and leaf fall (all leaves dropped) were recorded for all individuals sampled. An individual was considered to be fully leafed between the dates of flower flushing and leaf fall. We counted total flower and fruit production for each individual except for *C. pentandra* for which flower and fruit production were estimated based on the percentage of cover of the crown (Fournier, 1974). Using flower counts, we estimated the number of individuals in the population that were blooming for each sampling date. An individual was considered to be blooming if flower production on any sampling date exceeded 10% of total flower production for that individual. Flowering period was divided into (1) beginning, <50% of the population blooming; (2) peak, 51–100% of the population blooming; and (3) end, <50% of the population blooming. We also estimated the number of individuals in the population that matured fruits for each sampling date.

Intraspecific comparisons in flowering phenology—To determine if the intensity and duration of the dry season affect the flowering phenology of bombacaceous species, we compared intraspecific flowering overlap between study sites in different geographic locations with different precipitation regimes. Flowering overlap was estimated by pairwise comparisons of flowering intensity between sites. Flowering intensity for each species was determined as the percentage of trees flowering at each sampling date. Flowering overlap was estimated for *C. pentandra* between all three sites and for *C. aesculifolia* between Chamela-Cuixmala and Guanacaste. Flowering overlap was also estimated for *Pseudobombax septenatum* between Guanacaste and Osa. An overlap index (Pianka, 1973) was calculated for each species comparing flowering intensity between all pairwise combinations of sites. To determine if flowering overlap indexes differed statistically from random expectations (i.e., Pianka's index differed statistically from zero), a null model analysis was used to compare the mean overlap index with 1000 randomly simulated values (Kochmer and Handel, 1986; Wright and Calderón, 1995). Simulated values were generated by randomly sampling flowering intensities between dates for each species while maintaining the overall length of the flowering season constant. Flowering overlap was considered to occur when the observed index was larger than 95% of the 1000 simulated values. All calculations were performed using the EcoSim 7.0 computer program for null model analysis in community ecology (Gotelli and Entsminger, 2001).

To study the variation in flowering and fruiting of *C. pentandra*, which has been described as having a supra-annual flowering cycle, we estimated the variation in reproduction by comparing the number of trees flowering over three years (1999, 2000, 2001) at the three study sites (except for Osa in 1999). Logistic regressions (Stokes et al., 2000) were used to determine the effect of site and year on flowering and fruiting probability. Site and year were used as the independent variables, and the response variables were the number of trees in flower and the number of trees that matured fruits.

Interspecific comparisons in flowering phenology—To determine the importance of pollinator competition in bombacaceous trees, we compared interspecific flowering overlap between different species within each study site. Pianka's index (Pianka, 1973; Pleasants, 1990) was used to assess flowering overlap between all pairwise combinations of species co-occurring within

each site. The level of significance of Pianka's index was determined by the same procedure and assumptions previously described for intraspecific comparisons.

Estimation of pollinator use of floral resources—To estimate the importance of bombacaceous species in the diet of frugivorous and nectarivorous bats in Chamela-Cuixmala, mist-net sampling was conducted every 2 wk during the flowering of bombacaceous plants (November 2000 through June 2001). One 12-m and one 9-m mist net were placed in natural corridors in areas near bombacaceous species in flower and were opened for 4 h beginning at dusk. We collected pollen samples from the bodies and faces of all frugivorous and nectarivorous species captured using the glycerine-fucsin gelatin technique of Beattie (1971). For individuals that had no pollen on their bodies, fecal samples were collected. Each fecal sample was mixed with 2.5 mL of 70% alcohol and slides were made with this material. Pollen was identified using pollen keys (Lozano-García and Martínez-Hernández, 1990; Roubick and Moreno, 1991) and our own reference collection, developed during the study from flowers in the region that previously had been described as bat-pollinated or flowers that appeared to have bat-syndrome characteristics. All species of pollen were identified for each gelatin and fecal sample, and the most common was considered the principal pollen for that sample. In all cases, the most common pollen accounted for more than 80% of the pollen grains in the sample.

RESULTS

Effect of intensity and dry season duration on phenology (intraspecific variation)—Average annual rainfall for the three years studied was 550 mm in Chamela-Cuixmala, 1227 mm in Guanacaste, and 3539 mm in Osa. The dry season lasted from November through June in Chamela with an average of 6.9 mm of precipitation per month (Table 1, Fig. 1e), while the dry season lasted from December through April in Guanacaste with an average of 0.3 mm of precipitation per month (Table 1, Fig. 2e). The seasonal moist forest of Osa had a dry season of 4 mo and received more rainfall over this period (118.3 mm/mo) than the drier sites of Chamela-Cuixmala and Guanacaste (Table 1, Fig. 3c).

In spite of the differences in dry season duration and average annual rainfall, intraspecific comparisons indicate that the distribution of flowering over time for *C. pentandra* was the same at the three study sites (Pianka's index 0.9530, $P < 0.001$). Similarly, *Pseudobombax septenatum* flowered at approximately the same time in Guanacaste and Osa (Pianka's index 0.9516, $P < 0.001$). In contrast to this pattern, *C. aesculifolia* flowered later in Chamela-Cuixmala than in Guanacaste (Pianka's index 0.3815, $P < 0.467$), but at both sites this was the last species of Bombacaceae to flower at the end of the dry season.

In addition to studying intraspecific phenological patterns of trees of the family Bombacaceae at the three sites during 1 yr,

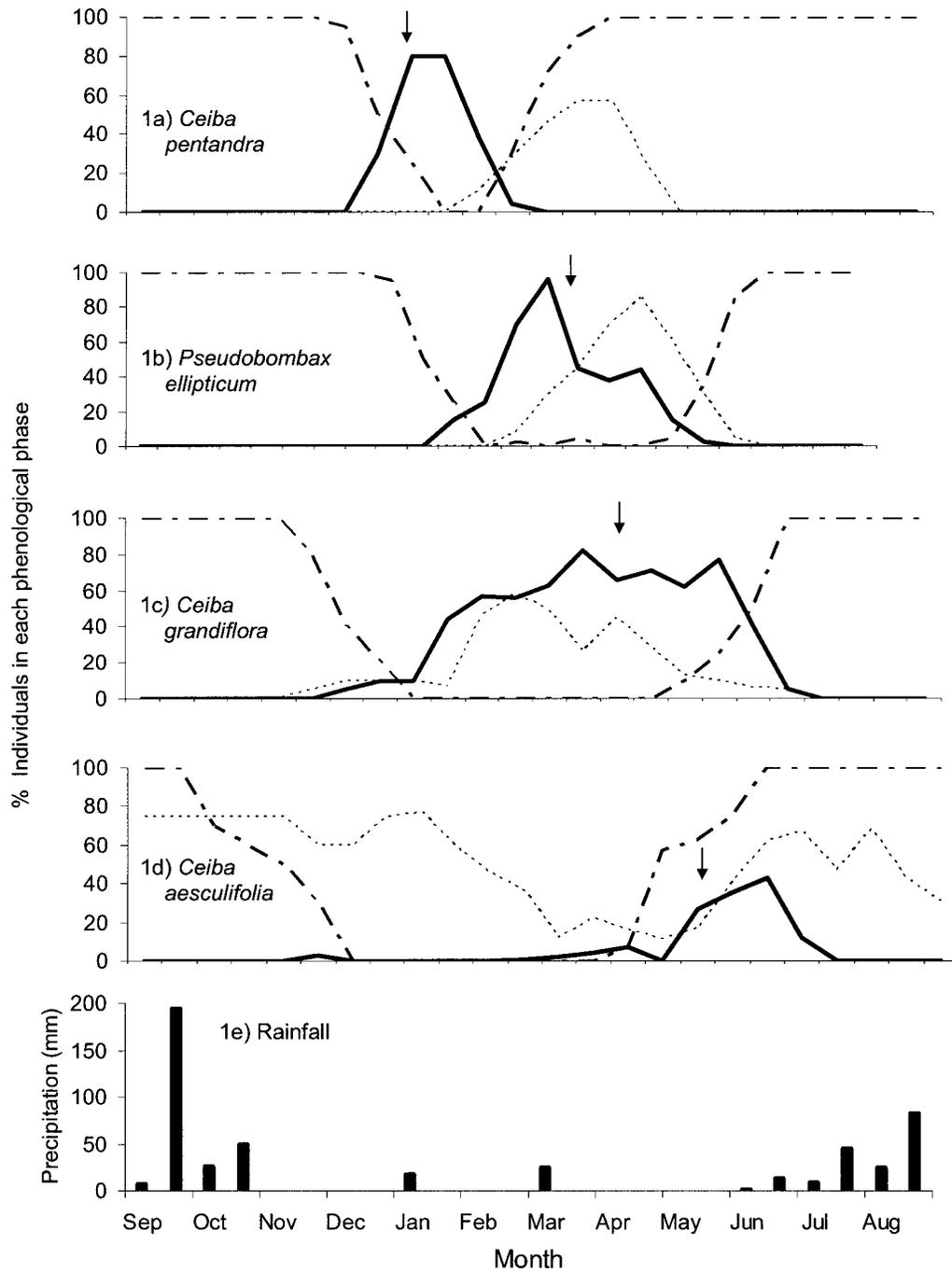


Fig. 1. (a–d) Phenological patterns of vegetative and reproductive parts of bombacaceous species and (e) total precipitation in the Chamela-Cuixmala Biosphere Reserve, Mexico. Percentage of individuals with flowers (—), leaves (---), and fruits (----) was calculated every 15 d from September 2000 to April 2001. Arrows indicate peak flowering for each species, calculated as the period with the greatest percentage of individuals in peak flower.

we compared the flowering frequency and fruit production of individuals of *C. pentandra* at the three sites for three consecutive years (1999–2001). *Ceiba pentandra* had a supra-annual blooming frequency. The percentage of individuals that flowered and matured fruits of *C. pentandra* varied depending on the site and the year (Table 2). The greatest reproductive success was observed in 1999 at Chamela-Cuixmala when approximately 100% of the individuals matured fruits. The lowest reproductive success was recorded in Guanacaste in 2000,

when only 21% of the studied individuals matured fruits, and in Osa in 2001, when only 21% matured fruits. A logistic regression analysis (Stokes et al., 2000) shows that *C. pentandra* differed in flowering frequency at the three sites over the years. During the three years studied, individual trees at Chamela-Cuixmala tended to flower more frequently than trees in Guanacaste (odds ratio of the probability of flowering = 8.4, 95% confidence interval [CI]: 3.26–21.73) and Osa (odds ratio = 7.87, 95% CI: 3.10–20.00). However, there are no differ-

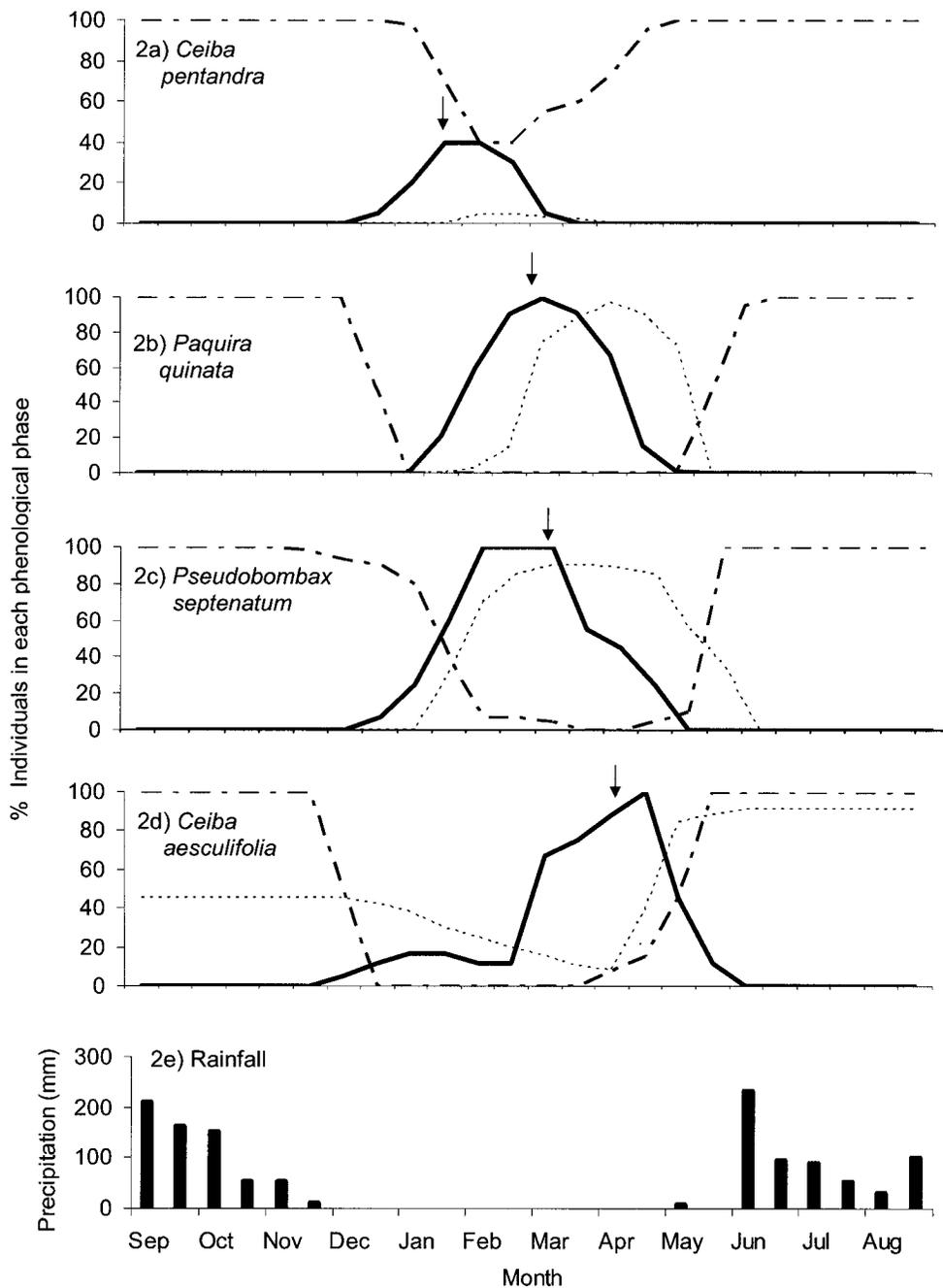


Fig. 2. (a–d) Phenological patterns of vegetative and reproductive parts of bombacaceous species and (e) total precipitation in Guanacaste, Costa Rica. Percentage of individuals with flowers (—), leaves (---), and fruits (----) was calculated every 15 d from September 2000 to April 2001. Arrows indicate peak flowering for each species, calculated as the period with the greatest percentage of individuals in peak flower.

ences in the flowering frequency between Guanacaste and Osa (odds ratio = 1.06, 95% CI: 0.55–2.06). The probability of flowering in *C. pentandra* was greater in 1999 in Guanacaste and Chamela-Cuixmala compared to 2000 (odds ratio = 7.14, 95% CI: 2.32–25.00) and 2001 (odds ratio = 9.41, 95% CI: 3.14–25.22).

Interspecific variation—The flowering period of the four species studied in Chamela-Cuixmala was restricted to the dry season and the general pattern was sequential flowering (Fig. 1) from December through June. *Ceiba pentandra* bloomed

from December through February, with a peak in January (Fig. 1a). *Pseudobombax ellipticum* flowered from January through May, with a peak in the beginning of April (Fig. 1b). *Ceiba grandiflora* was the first species that began flowering in December, approximately 2 mo after the beginning of the dry season, and exhibited a pattern of extended flowering continuing until the middle of June; peak flowering for this species was observed in April (Fig. 1c). *Ceiba aesculifolia* was the last species to begin flowering in April through July, with a peak in May (Fig. 1d). The Pianka overlap index shows that flowering distribution is distinct between all pairs of species

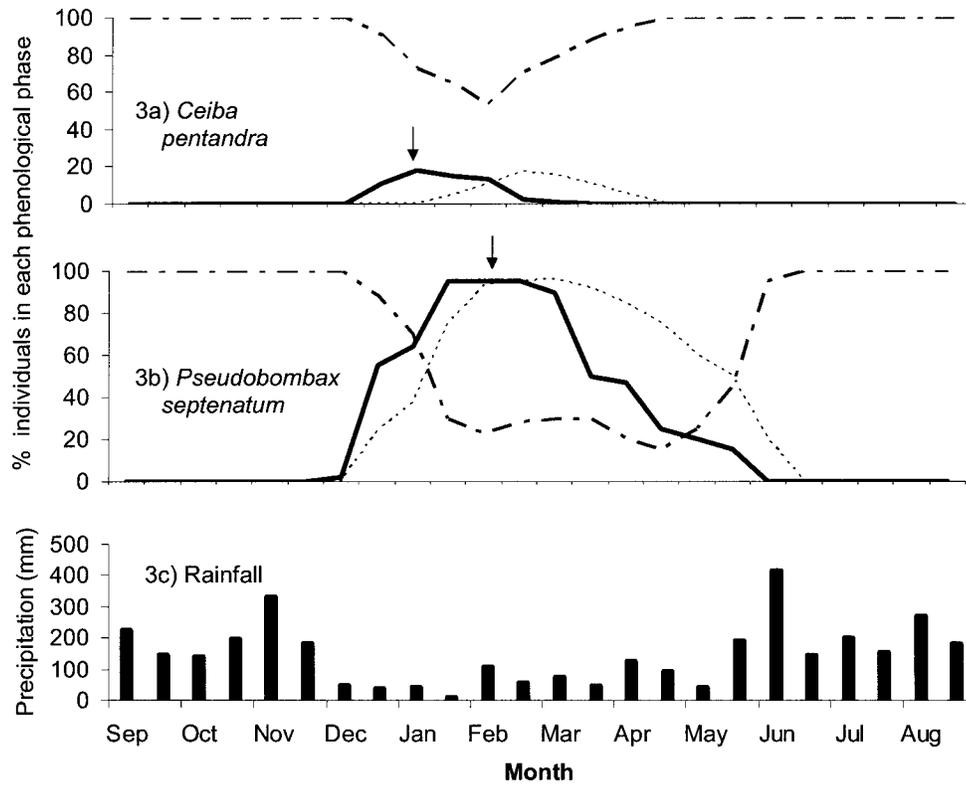


Fig. 3. (a–b) Phenological patterns of vegetative and reproductive parts of bombacaceous species and (c) total precipitation in the Osa Peninsula, Costa Rica. Percentage of individuals with flowers (—), leaves (---), and fruits (· · · · ·) was calculated every 15 d from September 2000 to April 2001. Arrows indicate peak flowering for each species, calculated as the period with the greatest percentage of individuals in peak flower.

except for *C. grandiflora* and *P. ellipticum*, which both show a peak in flowering the beginning of April (Table 3a).

The flowering period in Guanacaste also was restricted to the dry season, and species followed a sequential flowering pattern (Fig. 2), *Ceiba pentandra* flowered from December through February, with a peak in January (Fig. 2a). *Paquiria quinata* flowered from January through May, with a peak in March (Fig. 2b). *Pseudobombax septenatum* was the first species to bloom at the beginning of the dry season in December and continued flowering until the end of the dry season;

blooming peaked in March (Fig. 2c). A few individuals of *C. aesculifolia* initiated flowering in December, but the peak flowering did not occur until May, towards the end of the dry season. Given the extended flowering period of *P. septenatum*, the Pianka overlap index shows overlapping in the flowering

TABLE 2. Number of *Ceiba pentandra* trees at each site that failed to flower (No flower), produced flowers (Flower), and matured fruits (Fruit) over years shown.

Site	No flower	Flower	Fruit	Total ^a
1999				
Guanacaste	4	18	16	22
Chamela	1	27	27	28
2000				
Guanacaste	23	10	7	33
Osa	16	13	13	29
Chamela	1	10	4	11
2001				
Guanacaste	22	13	10	35
Osa	47	20	14	67
Chamela	5	16	12	21

^a Total number of trees includes the categories No flower and Flower, because all trees that matured fruits are a subgroup of the trees that also produced flowers.

TABLE 3. Observed pairwise flowering overlaps for four coexisting species in Chamela-Cuixmala, Mexico (a) and Guanacaste, Costa Rica (b) calculated using Pianka's (1973) overlap index. The number in parenthesis indicates the probability for the null hypothesis of no flowering overlap. Flowering overlap is indicated by values statistically larger than 0 ($P < 0.05$).

a)			
Species	<i>Ceiba grandiflora</i>	<i>Ceiba aesculifolia</i>	<i>Ceiba pentandra</i>
<i>Ceiba aesculifolia</i>	0.316 (0.776)		
<i>Ceiba pentandra</i>	0.570 (0.080)	0.012 (0.960)	
<i>Pseudobombax ellipticum</i>	0.840 (0.004)	0.432 (0.400)	0.211 (0.710)
b)			
Species	<i>Ceiba pentandra</i>	<i>Pseudobombax septenatum</i>	<i>Pachira quinata</i>
<i>Pseudobombax septenatum</i>	0.899 (0.001)		
<i>Pachira quinata</i>	0.502 (0.367)	0.762 (0.045)	
<i>Ceiba aesculifolia</i>	0.253 (0.970)	0.411 (0.815)	0.766 (0.081)

TABLE 4. Species of pollen found on the bodies and in fecal samples from nectarivorous bats (*Leptonycteris curasoae*/*Glossophaga soricina*^a) from November 2000 through June 2001 in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. Numbers indicate the quantity of samples with that species as the most common pollen each month. Asterisks indicate other months during which each species was consumed. Numbers in boldface type indicate the most important species each month.

Family and species of pollen	November	December	January	February	March	April	May	June
Agavaceae								
<i>A. colimana</i>	9/0 ^a	27/0	2/0	1/0				
Amaranthaceae								
Species 1						0/1		
Bignoniaceae								
<i>Crescentia alata</i>								6/21
Bombacaceae								
<i>Ceiba aesculifolia</i>							106/34	23/15
<i>C. grandiflora</i>	20/0	54/0	4/1	3/0	11/6	86/7	1/0	2/0
<i>C. pentandra</i>			75/3	0/2				
<i>Pseudobombax ellipticum</i>			21/0	77/0	120/0	1/1	0/2	
Cactaceae	4/0		1/0	3/0	4/0	4/0	0/2	0/3
Caesalpinaceae								
<i>Bauhinia pauletia</i>	102/0	4/0						
<i>B. unguolata</i>	1/0	15/1	13/0	1/0				
Combretaceae								
<i>Combretum</i> sp.			1/0	0/1		*		
Convolvulaceae								
<i>Ipomea ampullacea</i>	2/0	21/1	9/1			2/0		
Cucurbitaceae								
<i>Cucurbita argyrosperma</i>	6/0							
Mimosaceae								
<i>Albizia occidentalis</i>						1/0		
<i>Calliandra formosa</i>	2/0							
<i>Inga vera</i>					4/0			
Moraceae								
<i>Brosimum alicastrum</i>	2/0							
Sterculiaceae								
<i>Helicteres baruensis</i>	11/0	1/0	*					0/12
No pollen in sample	0/3	0/0	0/1	0/1	0/0	0/21	0/13	0/27
Number of samples	159/3	122/2	126/6	85/4	139/6	92/30	107/51	31/78

^a Numbers in data field separated by solidus refer to these bat species.

distribution of this species with *C. pentandra* and *P. quinata* (Table 3b). All other pairs of species are distinct and show different distributions in their peak flowering.

Similar to the pattern observed in Chamela-Cuixmala and in Guanacaste, in Osa *C. pentandra* flowered from December through February with a peak in January (Fig. 3a). *Pseudobombax septenatum* flowered from December through May with a peak in March (Fig. 3b). Flowering of *P. septenatum* overlapped with the flowering distribution of *C. pentandra* (Pianka's index 0.791, $P < 0.05$) at this site.

Seasonal pollinator use of floral resources—In Chamela-Cuixmala, pollen of bombacaceous species was not found on any of the frugivorous species sampled: *Artibeus intermedius* ($N = 84$), *A. jamaicensis* ($N = 416$), *A. lituratus* ($N = 30$), *A. phaeotis* ($N = 40$), *A. toltecus* ($N = 3$), and *Centurio senex* ($N = 9$). *Leptonycteris curasoae* was the most important pollinator of bombacaceous trees at Chamela-Cuixmala, and *Glossophaga soricina* was the second most important (Table 4). Bombacaceous species were the principal pollen found in samples from *L. curasoae* during 8 mo of the year, comprising

13% of the samples in November, 44% in December, 79% in January, more than 90% from February to April, and 25% in June. Although *L. curasoae* consumed pollen from up to three species of bombacaceous trees during 1 mo, one species generally made up the majority of the samples. In November and December 100% of the bombacaceous samples were *Ceiba grandiflora*, in January 75% were *C. pentandra*, in February 96% were *Pseudobombax ellipticum*, in March 91% were *P. ellipticum*, in April 100% were *C. grandiflora*, in May 99% were *C. aesculifolia*, and in June 92% were *C. aesculifolia*.

DISCUSSION

Our study indicates that trees of the family Bombacaceae from three sites with different precipitation regimes abscised their leaves at the beginning of the dry season and flowered during the dry season (Figs. 1, 2, 3). Peak flowering of each species was temporally staggered during the dry season in Guanacaste and Chamela-Cuixmala. These results first indicate that species of the family Bombacaceae respond to a general proximate environmental signal associated with the dry season

for leaf abscission. Second, the date and period of flowering and fruiting of each species was similar between sites with different dry season intensity and duration, indicating that fixed precipitation levels did not trigger flowering in these species. Third, the same species flowered at similar times in Mexico and Costa Rica, supporting one of the predictions of the phylogenetic hypothesis that historical constraints may be affecting phenological patterns (Kochmer and Handel, 1986; Wright and Calderón, 1995). Finally, flowering between tree species within different sites had little overlap, with the exception of *C. grandiflora* in Chamela and *P. septenatum* in Guanacaste, suggesting that competition for pollinators is a strong selective force that influences the staggered flowering pattern within this family. This selective pressure may have caused divergence in flowering time between species of similar taxa, thus modifying historical constraints related to this trait.

Effect of intensity and dry season duration on phenology (intraspecific variation)—The intraspecific comparisons showed that the same species flowered at similar times between sites in spite of different rainfall regimes. Flowering of *C. pentandra* initiated in December in Chamela-Cuixmala and in Guanacaste. In Chamela-Cuixmala this was approximately 3 mo after the dry season began, while in Guanacaste this was only about 1 mo after the beginning of the dry season. Similarly, in Osa *C. pentandra* began flowering in December (immediately after the beginning of the dry season) even though average monthly rainfall contrasted considerably with Chamela-Cuixmala and Guanacaste (Table 1, Figs. 1–3). The flowering pattern of *C. pentandra* is supra-annual in tropical wet forests, where individual trees have flowering and fruiting cycles with several years between blooming (Frankie et al., 1974; Newstrom et al., 1994; Gribel et al., 1999). This pattern is more common in Costa Rica, but it is not the case in Mexico, where trees flowered and set fruit almost every year (Table 2). In addition, there is annual variation in reproductive success between sites. However, regardless of the reproductive regularity of individuals, *C. pentandra* initiated flowering during a similar period of the year at the three sites.

Similarly, flowering began at the same time in Guanacaste and Osa for *P. septenatum* (i.e., December). Peak flowering of *C. aesculifolia* occurred in May at Chamela and in Guanacaste, and it was the last species of Bombacaceae to flower at both sites (i.e., end of the dry season). Several phenological studies have concluded that changes in water availability from shifts in precipitation regimes and soil moisture are the essential proximate causes affecting phenological patterns (Opler et al., 1976; Reich and Borchert, 1984; Borchert, 1994). However, few of these studies have compared the same species in contrasting environments. Our data suggest that the flowering period of bombacaceous species is not determined by precipitation. Moreover, levels of soil moisture between these sites vary greatly. In Osa, the most superficial levels of soil remain saturated during the wet season and the first months of the dry season (December and January), and the water deficit is 0 or very small during this period (Gómez and Herrera, 1985). In contrast, in the dry forest of Guanacaste there is a significant level of water deficit in the beginning of the dry season (Gómez and Herrera, 1985), and in the case of Chamela-Cuixmala soil water content is completely dry from January through June (Galicía et al., 1999). Because bombacaceous species have the ability to store water in their trunks (Wangaard et al., 1954; Borchert, 1994), intensity and duration of the dry season

and soil water content do not appear to restrict flowering to a particular period during the dry season.

Interspecific variation—The interspecific comparisons within sites showed a pattern of sequential flowering with the exception of *C. grandiflora* in Chamela-Cuixmala and *P. septenatum* in Guanacaste (Figs. 1–3). In the case of *C. grandiflora*, the extended flowering period can be explained by a relatively low number of flowers produced each day (Quesada et al., 2003), thereby distributing the reproductive effort over a longer period of time and producing an overlap with other species. *Pseudobombax septenatum* also demonstrated an extended flowering period with fewer flowers produced at the beginning and the end of the flowering period; however, unlike *C. grandiflora*, a massive flowering occurred in the middle of the dry season. Although *P. septenatum* overlapped with *C. pentandra* at the beginning and with *P. quinatum* at the end, the massive peak of flowering occurred between the peaks of these other two species (Fig. 2).

Several evolutionary hypotheses have been proposed to explain staggered flowering of plants. One of the first ideas to be suggested was that plants with the same pollinators will avoid competition through staggered flowering and thus will increase their reproductive success by attracting more pollinators (Robertson, 1895). This hypothesis has been supported by empirical evidence that establishes a relationship between the staggered flowering patterns of plants with their hummingbird pollinators (Stiles, 1975; Feinsinger, 1978). Another hypothesis states that staggered flowering avoids the transfer of interspecific pollen that may cause pollen loss, reduction of receptive stigma surfaces, and overall lower reproductive success (Thomson et al., 1981). These hypotheses are not mutually exclusive, and both may partially explain the staggered flowering observed in bombacaceous species. Therefore, competition for pollinators and avoidance of interspecific pollen deposition are important ultimate factors that will selectively favor staggered flowering of species within the same family having the same pollinators.

Another factor that may affect phenological patterns in the bombacaceous species studied is timing of seed dispersal. Most of the species matured fruits shortly after flowering and dispersed their seeds during the dry season both in Costa Rica and Mexico, occurring at the best time for wind dispersal (i.e., dry and windy). The only exception is *C. aesculifolia*, which flowered at the end of the dry season both in Guanacaste and Chamela and dehisced mature fruits during the following dry season (Fig. 2). This is the only Neotropical bombacaceous species with a fruiting pattern that belongs to a previously described group of “dry season fruiterers” (Frankie et al., 1974). This pattern suggests that seed dispersal may be an important ultimate factor that constrains the flowering period of these bombacaceous trees.

The species in the family Bombacaceae used in our study have been classified within the functional group of deciduous trees with low-density wood and high-stem water storage (Borchert, 1994). According to this classification, water deficits trigger leaf shedding followed by flowering for prolonged periods. Our results are not consistent with this hypothesis. Although all species of trees of the family Bombacaceae shed leaves at the beginning of the dry season, flowering and fruiting patterns are staggered throughout the dry season in the dry forests of Mexico and Costa Rica. Therefore, the loss of leaves is likely to be correlated with the relative high minimum leaf

water potential and low-density wood of these species (Holbrook et al., 1995), but it is not directly involved in triggering the sequence of flowering or fruiting. Inter- and intraspecific variation in flowering and fruiting is consistent for most tree species at both sites. Wright and Cornejo (1990) showed that even when soil water potential is maintained at field capacity during the dry season, the timing of leaf fall of deciduous trees of low-density wood and high-density wood is not affected.

Seasonal pollinator use of floral resources—Our data suggest that competition for pollinators is, perhaps, one of the most important ultimate factors affecting the phenological patterns observed in the family Bombacaceae in the Neotropics. In Chamela-Cuixmala, trees of the family Bombacaceae were a main resource for the nectar-specialist *Leptonycteris curasoae* during 8 mo, and this bat generally concentrated on one bombacaceous species each month. The more generalist nectarivore, *Glossophaga soricina*, utilized bombacaceous species during 6 mo and also concentrated on one bombacaceous species each month. The sequential use of bombacaceous species by bats coincided with the flowering phenology of these species. These data support the idea that flowering phenology is staggered to avoid competition for pollinators as has been suggested by various authors (Janzen, 1967; Stiles, 1975; Feinsinger, 1978). It is especially important for bombacaceous species to avoid competition for pollinators since they have been described principally as self-incompatible (Hamrick and Murawski, 1990; Gribell et al., 1999; Quesada et al., 2001, 2003) and therefore are completely dependent upon pollinators to achieve fruit set. Furthermore, greater pollinator attraction during peak flowering in species with synchronous blooming (i.e., *Ceiba pentandra*, *C. aesculifolia*, *Pachira quinata*, and *Pseudobombax septenatum*) favors higher levels of outcrossing (Stephenson, 1982; Quesada et al., 2003).

In conclusion, our study suggests that phenological patterns of the Bombacaceae family in Neotropical dry forests are mainly constrained by adaptive selective pressures associated with competition for pollinators and phylogenetic membership. Abiotic factors related to precipitation and soil water content appear to be regulating leaf flush and abscission of leaves, but the principal causes of flowering are related to ultimate factors associated with competition for pollinators. This study is the first that evaluates the phenological pattern of species and genera of the same family at different latitudes in a similar life zone. Future studies should evaluate other taxonomically related groups found in similar habitats but different regions to further test the conclusions of our study.

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