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Photoperiodic control of seasonal development and dormancy in tropical stem succulent trees

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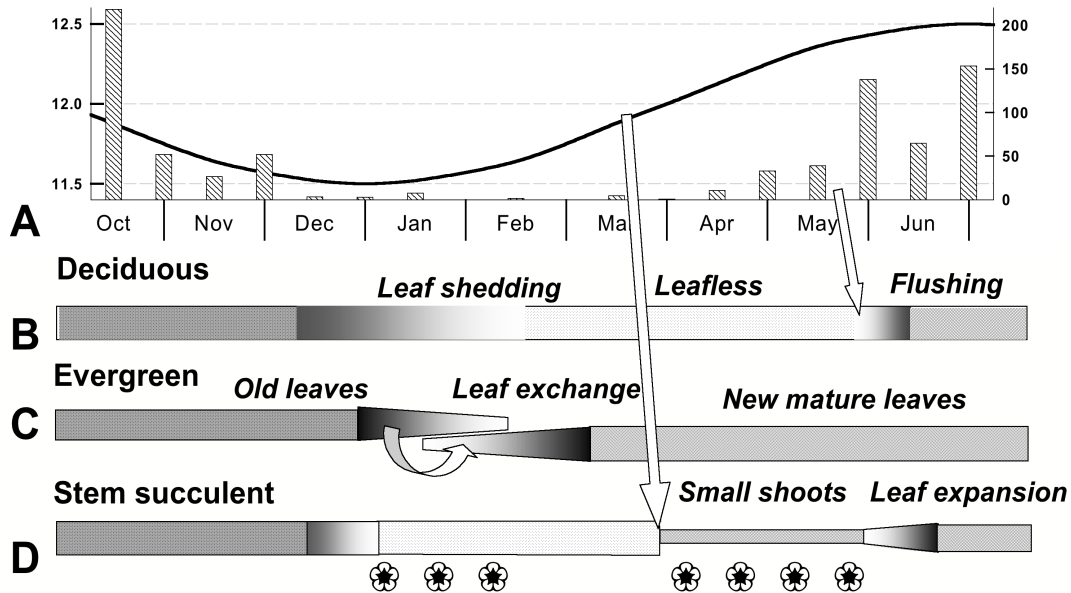
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Summary Tropical stem succulent trees store large quantities of water in their trunks yet remain leafless during the early and mid-dry season. In contrast to most other tropical trees, bud break of vegetative buds is not induced in fully hydrated stem succulents between the winter solstice and the spring equinox by leaf abscission, abnormal rain showers or irrigation. Vegetative buds of leafless trees are therefore in a state of endo-dormancy similar to that of temperate perennial plants during early winter. Highly synchronous bud break regularly occurs soon after the spring equinox, often weeks before the first rainfalls of the wet season. These observations suggested that endo-dormancy and bud break might be induced by declining and increasing photoperiods after the autumn and spring equinoxes, respectively. In phenological field observations we confirmed the highly synchronous bud break after the spring equinox in many trees of five stem succulent species in the northern and southern hemisphere. Shoot growth of potted saplings of *Plumeria rubra L.* was arrested by a decline of daylength below 12 h after the autumn equinox, but continued in saplings maintained in a 13-h photoperiod. Inversely, exposure to a 13-h photoperiod induced bud break of dormant apical buds in saplings and cuttings in January, when plants in natural daylength of < 11.7 h remained dormant. Photoperiodic control of endo-dormancy of vegetative buds in stem succulents is thus supported by field observations and experimental variation of the photoperiod. At low latitudes, where annual variation of daylength is less than one hour, bud dormancy is induced and broken by variations in photoperiod of less than 30 min.

Introduction

Because of the absence of distinct seasonal variation in temperature, the time course of seasonal development of tropical trees is mainly determined by the duration and severity of the dry season (Borchert 1994a, 2000). For example, in Guanacaste, Costa Rica, up to 95% of the annual rainfall, ranging from 900 to >2000 mm, occurs between May and November (Figure 1A; Borchert 2000). In analogy to the synchronization of shoot growth periodicity of temperate trees by low winter temperatures, one might expect tree development in tropical forests to be synchronized by such a long, severe dry season. Actually, such forests constitute mosaics composed of several functional tree types that are adapted to seasonal drought in different ways. Deciduous species shed their mesic leaves during the early dry season, remain strongly desiccated during the remainder of the dry season (stem water potentials of -5 to -7 MPa) and flush synchronously after the first major rains have caused rehydration of the top soil during the early wet season (Figure 1 B arrow; Borchert 1994a). Evergreen, leaf exchanging species shed their old, progressively desiccated leaves during the early or mid-dry season, and new shoots emerge immediately after or shortly before leaf abscission is complete (Fig 1 C; Borchert 1994a, 2000; Borchert et al. submitted). Such species are confined to microsites with good soil water storage, which enables trees to rehydrate during leaf shedding. The vegetative phenology of deciduous and leaf-exchanging species is thus mainly determined by seasonal variation in tree water status (Borchert 1994a, 2000).

Figure 1. Seasonal variation in environmental factors (A – rainfall, daylength) and phenology of deciduous, evergreen and stem succulent trees (B-D) in the semideciduous forest of Guanacaste, Costa Rica. Arrows indicate postulated causes for vegetative bud break. Characteristic flowering periodicity is shown for stem succulents only.



Deciduous, stem succulent tree species, which often occupy the driest sites in tropical dry forests, store large quantities of water in the extensive parenchyma tissues of their trunks and thus have a relatively low wood density ($<0.5 \text{ g cm}^{-3}$; Borchert 1994a). They maintain high stem water potentials throughout the dry season ($> -0.5 \text{ MPa}$; Borchert 2000; Borchert et al. submitted). Leaves are usually shed rapidly during the early dry season without being water stressed (Figure 1 D, Dec). Well-hydrated trees remain leafless for several months, but flower buds may open gradually during the early dry season (Figure 1 D Jan-Feb). Bud break of vegetative buds generally occurs in April, weeks before the first major rains (Figure 1 D). Thus, in contrast to deciduous and leaf-exchanging species, there is no evidence for the control of vegetative phenology by seasonal variation in tree water status. The central questions posed by the phenology of stem succulents are therefore: What causes bud break during the late dry season, in the absence of any significant rainfall? Why does bud break in water-saturated twigs not take place shortly after leaf abscission, as it does in rehydrated leaf exchanging species (Figure 1 C)? What causes the rapid shedding of well hydrated leaves during the early dry season?

In more than 25 tropical tree species highly synchronous flowering after the autumn equinox was found to be induced by a decline in photoperiod of 30 min or less (Borchert 2000, Rivera and Borchert 2000). These observations alerted us to the fact, that synchronous developmental change occurring after the autumn or spring equinox in the absence of notable changes in seasonal climate is likely to be induced by declining or increasing photoperiod, respectively. In the stem succulents *Bursera simaruba* and *Pseudobombax septinatum* highly synchronous bud break with low inter-annual variation regularly occurs after the spring equinox (Figs. 1 D; 2). The wide-ranging paleotropical *Bombax malabaricum* flushes in April and October in the northern and southern hemisphere, respectively (Troup 1921, Coster 1923, Koelmeyer 1959). Collectively these and other observations suggest that synchronous bud break of stem succulent species during the late dry season is induced by increasing daylength (Figure 1 D arrow) and, implicitly, that bud dormancy is induced

and maintained by photoperiods shorter than 12 h. In this study we combine our own field observations and experiments with the analysis of published phenological records of stem succulent trees to support the proposed hypothesis.

Table 1. Species of tropical stem-succulent trees mentioned in the text. References for observations reported in the literature: A - Borchert 1996; B - Bullock and Solis-Magallanes 1990; C - Coster 1923, Holttum 1940, Koelmeyer 1959; D - Frankie et al 1974; E - Lawton and Akbar 1968; F - Murashige 1966; G - Windsor 1982; H - Baum 1995; Wickens 1983; J - Njoku 1964.

<i>Family/Species</i>	<i>Place observed</i>	<i>Figure</i>	<i>Reference</i>
Anacardiaceae			
<i>Spondias purpurea</i> L.	Costa Rica, Mexico		A, B
Apocynaceae			
<i>Plumeria rubra</i> L.	Costa Rica, Mexico, Nigeria	3, 4, 6-8	B, E
<i>Plumeria acuminata</i> Ait.	Hawaii		F
Bombacaceae			
<i>Adansonia sp.</i>	Africa, Madagascar, Hawaii		H
<i>Bombax malabaricum</i> DC.	India, Ceylon, Singapore, Java	5	C
<i>Bombacopsis quinatum</i> (Jacq.) Dugand	Costa Rica		D
<i>Chorisia insignis</i> (Kunth) P.E. Gibss & Semir	Argentina		
<i>Pseudobombax septinatum</i> (Jacq.) Dugand	Costa Rica, Panama	2	A, G
<i>Pseudobombax argentinum</i> (Fries) Robyns	Argentina		
Burseraceae			
<i>Bursera simaruba</i> (L.) Sarg.	Costa Rica, Mexico	3, 4	A, B
Cochlospermaceae			
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Costa Rica		A
Sterculiaceae			
<i>Hildegardia barteri</i> (Mast.) Kosterm.	Nigeria		J

Materials and methods

Tree species. Stem succulent species observed in the field or mentioned in the text are listed in Table 1. In the text species will be referred to by genus name, unless several congeneric species are discussed.

Phenological field observations. Phenological field observations of stem succulents and experimental work with *Plumeria* were prompted by the observation of synchronous flowering of many trees of several species in autumn 1997 (Borchert 2000, Rivera and Borchert 2000) and of many *Plumeria* in April 1998, which suggested photoperiodic control (see Results). Field observations in Guanacaste, Costa Rica were designed to be completed before the termination of our research project in spring 1999. In summer 1998 40-80 trees of *Bombacopsis*, *Bursera*, *Plumeria* and *Spondias* were identified, flagged with plastic tape and mapped. To facilitate frequent observation, most trees were located close to highways and country roads within 40 km of Hacienda La Pacifica, Cañas, the site of related field studies (Borchert 1994, 2000, Rivera and Borchert 2000). Trees were monitored every 8 – 10 d between Nov 1998 and Jan 1999 for senescence and abscission of leaves and in Mar/May 1999 and 2000 for bud break and inflorescence development in *Bombacopsis*, *Bursera*, *Plumeria* and *P. septinatum*.

Field observations of *Chorisia* and *P. argentinum* were made in Argentina every two weeks from August 1998 to March 2000 at the lower altitudes of Calilegua National Park, Province of Jujuy (23° S). In this subtropical dry forest with 80 % deciduous species (Sarmiento 1972), less than 5 % of annual precipitation, ranging from 600-1400 mm, falls during the dry season between mid May and September.

Long-term flowering periodicity obtained from herbarium collections. We established earlier that species-specific flowering periods obtained from sufficiently large numbers of flowering herbarium collections are similar to those observed in phenological field studies (Borchert 1996). An abrupt increase in the number of flowering herbarium collections from one month to the next indicates low inter-annual variation in the onset of flowering of *Bursera* and *Plumeria* and, implicitly, a regular environmental trigger of inflorescence development (Figure 3; Borchert 1996, Rivera and Borchert 2000). The Herbarium of the Missouri Botanical Garden, St. Louis, Mo., was used to analyze inter-annual variation in flowering periodicity. Collection date and site of all flowering herbarium collections were recorded and flowering periodicity was graphed (Figure 3).

Experimental analysis of endo-dormancy in Plumeria. Experiments with *Plumeria* were prompted by the observation of synchronous flowering in spring 1998 and by the discovery of large numbers of 40-60 cm tall, shallow-rooted saplings at Playa Hermosa, Guanacaste. Experimental design was constrained by the limited facilities of our field laboratory and by the need to complete experiments by April 1999.

In July 1998, ~ 80 *Plumeria* bare-root saplings were collected at Playa Hermosa, planted in plastic bags containing 2 L soil and maintained in natural daylength near the field laboratory at Hacienda La Pacifica. Six 60 W fluorescent bulbs, half cool, half warm light, were mounted on a 2-m long beam 1.20 m above ground and shielded from rain by a 50 x 220 cm transparent corrugated plastic sheet. Experimental plants were placed on a plastic sheet covering the ground below the lights. Lights were turned on daily between 17.30 and 19.00 h by an electric timer (experimental night interruption, which would have disturbed neighbors, was not an option). With this light regime, daylength of treated plants varied between 12.45 and 13.00 h between the equinoxes, while natural daylength varied between 11.30 and 12.00 h (see Table 2).

Table 2. Natural and experimental variation in daylength during experimental modification of vegetative phenology in *Plumeria*:

Date	Dawn h	Controls		Experimental	
		Dusk h	Daylength h	Dusk h	Daylength h
21-Sep	6.00	18.00	12.00	19.00	13.00
21-Dec	6.15	17.45	11.30	19.00	12.45
21-Mar	6.00	18.00	12.00	19.00	13:00

Experimental treatments are described in the Results (Figure 7). In experiments with bagged saplings, 8 – 10 plants were used per treatment. Treated plants were illuminated as described in Table 2 and controls were kept in natural daylight at a site shielded from any artificial light source. Cuttings were prepared from the shoots of decapitated saplings, air-dried for 2 d to allow wound healing, and then placed upright in transparent plastic bags containing a few ml water. Bags were placed between the bagged saplings.

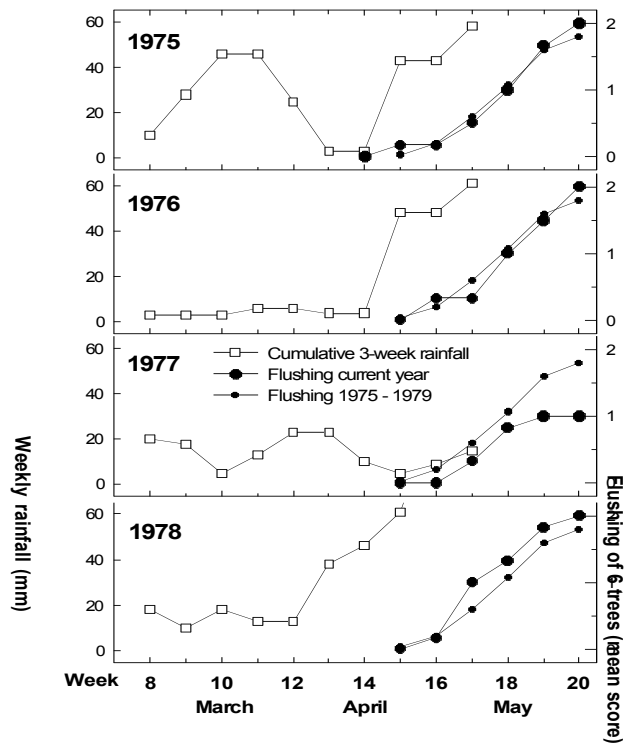
Results

In the following sections our observations on the control of bud dormancy in tropical stem succulent trees are combined with evidence reported in the literature.

Endo-dormancy of leafless stem succulent trees

The following observations indicate that bud break in leafless twigs of stem succulents is not inhibited by water stress. Because of the storage of large quantities of water in stems and twigs, stem succulents maintain stem water potentials > -0.5 MPa throughout the dry season (Borchert 2000, Borchert et al. submitted). During several years of observation at Hacienda La Pacifica in Guanacaste, *Bursera* and *Bombacopsis* growing at the edge of rivers or irrigation canals shed leaves in Dec and remained leafless for several months like their conspecifics at dry sites. An abnormal 70-mm rainfall in mid-February 1999 induced rapid flushing in all leafless deciduous and brevideciduous species, but not in any stem-succulent species except *Cochlospermum*, which normally flushes after the first heavy rains of the wet season (Borchert et al. submitted). Similarly, abnormal rainfall in Dec caused out-of-season flushing in leafless trees of all deciduous species in a Mexican dry forest, but not in any stem succulent trees of 10 species including *Bursera*, *Plumeria* and *Spondias* (Bullock and Solis-Magallanes 1990). In contrast to trees of all other functional types observed in Costa Rica, vegetative buds in leafless, water-saturated twigs of most stem-succulent species are thus unable to resume growth between December and late March. This indicates that during this period vegetative buds are in a state of endo-dormancy similar to that of buds of temperate trees during early winter (Borchert 1991, Crabbé and Barnola 1996). However, resting lateral flower buds of several stem succulent species of the Bombacaceae (e.g., *Bombacopsis*, *Bombax*, *Pseudobombax*; Coster 1923, Borchert 1996, Rivera, unpublished) and other families (e.g. *Spondias*; Borchert 1996) open gradually soon after leaf shedding during the early dry season, i.e., bud break occurs once lateral buds have been released from correlative inhibition by old leaves (Figure 1 D, Jan/Feb; Borchert 1991, 2000). Thus, at a time when terminal vegetative buds are dormant, lateral flower buds are not.

Figure 2. Flushing of *Pseudobombax septinatum* and cumulative 3-week rainfall observed from 1975 to 1978 on Barro Colorado Island, Panama. Data from Windsor (1982) and Stanley (1982).



Photoperiodic induction of bud break after the spring equinox

Synchronous bud break of vegetative buds

In a Mexican dry forest, bud-break in 10 stem-succulent species usually occurs in May, regardless of the absence or occurrence of rain, but shoot growth and leaf expansion remain arrested until after the first substantial rains (Figure 1 D; Bullock and Solis-Magallanes 1990). In Costa Rica, all observed trees of *P. septinatum* (>50) and *Bombacopsis* (>50) started flushing synchronously around April 10-15 and May 15-20, 2000, respectively. In Northern Argentina, synchronous bud break of *Chorisia* (40) and *P. argentinum* (20) was observed during mid-October in 1998 and 1999, six months out of phase with bud break in Central America. The wide-ranging, paleotropical *Bombax malabaricum* flushes in Apr and Oct in the northern (Troup 1921, Koelmeyer 1959) and southern hemisphere, respectively (Coster 1923 observed synchronous bud break of ~200 trees in Oct 1921 and 1922). In Southeast Africa most species of *Adansonia* (baobab) leaf out in Oct/Nov, shortly before the rainy season (Baum 1995). Two baobab trees cultivated in the National Tropical Botanical Garden at

Kauai, Hawaii, remained leafless and dormant throughout the rainy Jan-Apr, but started flushing in late April 2000.

The phenology of six *P. septinatum* was observed weekly on Barro Colorado Island in Panama. During five consecutive years synchronous shoot growth and leaf expansion started during the last weeks of April (Figure 2; Windsor 1982). The high time resolution of this unique data set permits the detailed analysis of the interaction between daylength and rainfall in the control of bud break and flushing. A comparison of the time course of leaf expansion in each year with its 5-yr mean illustrates the minimal inter-annual variation of synchronous bud break and flushing, which is a good indicator of photoperiodic induction of bud break. Rainfall of > 30 mm, generally sufficient to induce flushing of leafless tropical trees (Borchert 1994b), did not induce earlier than normal bud break and flushing of *P. septinatum* (Figure 2, weeks 9-10 in 1975), thus rainfall cannot be the cause of bud break. Flushing after bud break was rapid when preceded by rainfall exceeding 40 mm, but was slower than normal after unusually low cumulative rainfall in 1977. Thus, despite the large amounts of water stored in stem succulent trees, an adequate soil water supply appears to be required for shoot and leaf expansion. In Costa Rica and Mexico rainfall is very rare before photoperiodic induction of bud break in late April. Shoot and leaf expansion are therefore usually delayed until after the first heavy rains of the wet season (Figure 1 A, D; Bullock and Solis-Magallanes 1990).

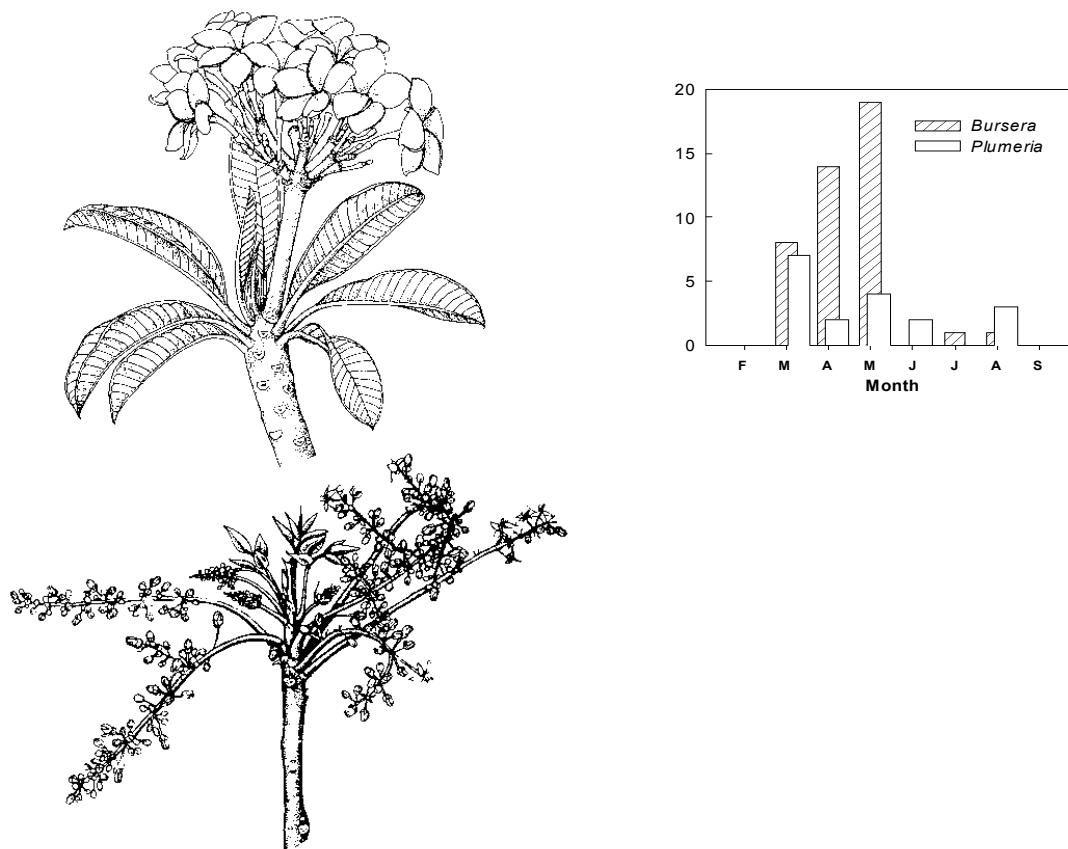


Figure 3. *Plumeria rubra* (top left) and *Bursera simaruba* (bottom left). Young annual shoots (redrawn from Kunkel 1978 and Tomlinson 1980) and flowering periodicity obtained from flowering herbarium collections in the herbarium of the Missouri Botanical Garden, St. Louis, Mo.

Synchronous initiation of inflorescence development

Bud break in *Bursera* is indicated by the rapid emergence of lateral inflorescences that form on the first, unexpanded, leafless nodes of new shoots. Young leaves are initiated on the following nodes and expand weeks after the inflorescences (Figure 3). The abrupt beginning and cessation of flowering indicated by flowering herbarium collections correspond to this developmental sequence (Figure 3 bottom). In 1999 and 2000, small inflorescences appeared during the first 10 days of April in all observed mature trees (>70). In contrast, we did not observe bud break during early April in any of the vigorous vegetative sprouts developing on heavily pruned *Bursera* trees used as living fences throughout Guanacaste.

During bud break of leafless, mature *Plumeria* small young leaves emerge slowly at the shoot apex, whereas a single lateral bud develops rapidly into a branched inflorescence, on which new flowers open for several months (Figure 3). Soon after bud break, mature trees are thus covered with conspicuous white flowers when emerging leaves are still very small. Flowering herbarium collections reflect this abrupt beginning of flowering in March and its continuation for many months (Figure 3 bottom). In early April 1998 and 2000 we observed from airplanes descending towards San José many leafless, flowering *Plumerias* growing at the steep slopes along rivers throughout the lower Central Valley of Costa Rica. In all *Plumerias* (> 60) observed on rocky slopes throughout Guanacaste, Costa Rica, the first flowers opened in early April 1999 and 2000. On young and mature trees, small leaves started expanding slowly in late March. In *Bursera* and *Plumeria* increasing daylength thus induces rapid, highly synchronous inflorescence development with low inter-annual variation, whereas early vegetative growth is slow or delayed.

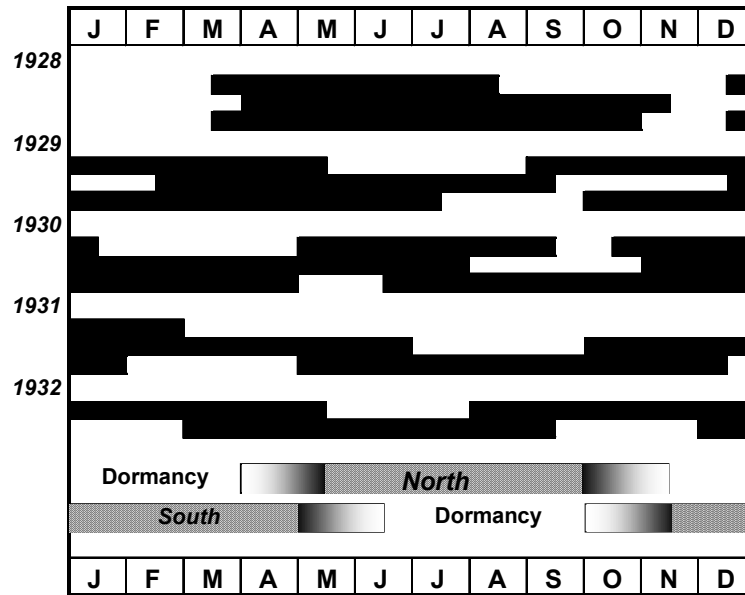


Figure 4. Shoot growth periodicity of *Bombax malabaricum* and *B. insigne* Wall.. Horizontal bars indicate period from flushing to leaf abscission. Empty spaces between bars indicate periods when leafless trees are dormant. Top: Shoot growth periodicity of one *B. insigne* and two *B. malabaricum* was observed from 1928 to 1932 at the Botanical Garden of Singapore (2° N; data from Holttum 1940). Bottom: shoot growth periodicity of *B. malabaricum* in the northern and southern hemisphere (India: Troup 1921; Ceylon: Koelmeyer 1959; Java: Coster 1923).

Asynchronous bud break at the equator

Shoot growth periodicity of two *Bombax malabaricum* and one *B. insignis* was observed every two weeks for nine years in the Botanical Garden of Singapore (2° N), located near the equator in a humid climate with minimal seasonal variation (Figure 4; Holttum 1940). During this period, bud break occurred during every month of the year and shoot growth periodicity varied widely among the three trees. In *B. malabaricum*, leaves were usually retained for 7-10 mo, and after leaf abscission the trees remained leafless for ~2 mo. Thus, all aspects of shoot growth periodicity, namely time of bud break, duration of shoot growth and leaf retention, and onset of dormancy, are clearly under endogenous control and the constant 12 h-photoperiod of Singapore permits bud break at any time. These observations suggest that the synchronization of bud break after the spring equinox, as observed in the northern and southern hemispheres (Figure 4 bottom), results from inhibition of meristem activity by photoperiods shorter than 12 h and its release by increasing photoperiods after the spring equinox. Synchronous bud break of *Bombax* at rather low latitudes (Ceylon: 7° N; Java: 7° S; Coster 1923, Koelmeyer 1959) indicates that a decline in daylength of 25 min or less is sufficient to arrest meristem activity.

Conclusions

Shoot growth periodicity of stem succulent trees shows consistently the characteristics predicted for induction of bud break by an increase in photoperiod above a critical daylength slightly longer than 12 h (Borchert 2000, Rivera and Borchert 2000). Bud break is not preceded by any notable climatic change; it is highly synchronous throughout a landscape and occurs after the spring equinox; it has minimal inter-annual variation and is 6 mo out of phase between the northern and southern hemisphere; it is asynchronous near the equator.

Experimental modification of shoot growth periodicity in stem succulents

Bud dormancy in cuttings of Bombax

In pioneering experiments done shortly before photoperiodic control of bud dormancy in temperate trees was recognized, Coster (1923) attempted to break bud dormancy in cuttings of *Bombax* by treatments used to force cuttings of temperate woody plants into precocious bud growth. He achieved bud break only exceptionally in cuttings made during the early and mid-dry season. However, in all cuttings prepared ~ 4 wk before flushing of trees in the field bud growth started within 3-4 wk in controls and treated cuttings alike. Coster concluded that bud break in intact trees and cuttings was induced by the same unknown environmental cue.

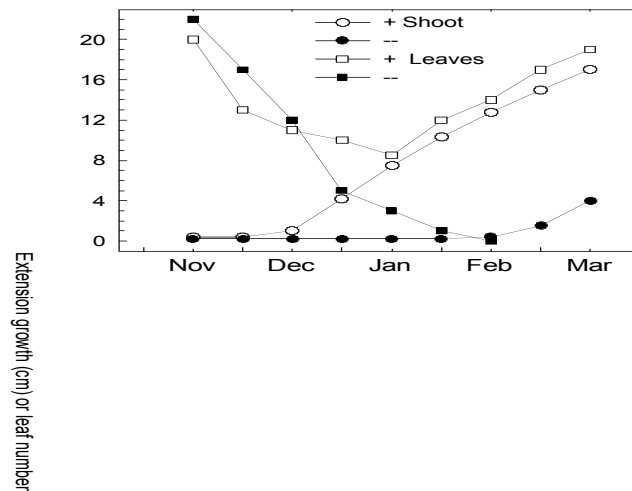
Breaking of dormancy in Plumeria trees by night interruption

In Ibadan, Nigeria (7° N), night interruption of 4 h from late Nov to Mar caused the resumption of arrested shoot growth in *Plumeria* trees within 4 wk after the beginning of the treatment (Figure 5; Lawton and Akpan 1968). Branches on control trees resumed shoot growth in early Mar, when daylength was ~12 min longer than the minimum. The classical experimental treatment of interrupting the long night associated with short photoperiods (Thomas and Vince-Prue 1997) thus induced bud break in December, three months earlier than in trees exposed to the natural increase in daylength.

Table 3. Phenology of *Plumeria* saplings transferred from the northern to the southern hemisphere.

<i>Date</i>	<i>Photoperiod</i>	<i>Phenology</i>
Jan 1999	> 14 h	Shoot growth and leaf formation
Apr/May '99	12 > 11 h	Leaf abscission
Oct '99	12 > 13 h	Shoot growth and leaf formation

Figure 5. Effect of a 4-hour night interruption on shoot growth and leaf retention of *Plumeria* trees growing in Ibadan, Nigeria (+ night interruption, - - control; data from Lawton and Akbar 1968).



Phenology of Plumeria seedlings transferred to the Southern hemisphere

Seven bare-root, leafless, 20-cm long *Plumeria* seedlings were taken from Costa Rica to Córdoba, Argentina (25° S) in Dec 1998, where they were kept indoors during the cold months June-August. After abnormal flushing in Jan 99, which was induced by the transfer to long photoperiods, leaf shedding and flushing were caused by changes in photoperiod around the autumn and spring equinox, respectively (Table 3).

Induction and breaking of dormancy of Plumeria by experimental variation of daylength

To observe the effect of declining daylength on shoot growth in *Plumeria*, potted saplings were decapitated 10 cm above ground in early Aug 1998, 7 weeks before the autumn equinox. The controls remained in natural, declining daylength, the daylength of the experimental group was extended to ~13 h (see Table 2). In all plants, release from apical dominance by decapitation induced the outgrowth of a single lateral bud near the cut end (Figure 6 A). Soon after the autumn equinox, when the new lateral shoots were 10 -15 cm long and had 4 - 6 small leaves, shoot growth was arrested in the controls and all leaves abscised during the next two months. In the experimental plants shoot growth and leaf expansion continued and shoots had 8 – 10 large leaves by Dec.

Effects of increasing daylength on bud break of terminal and lateral buds were studied in well-watered yet leafless – and hence dormant - potted saplings maintained under natural daylength since the autumn equinox. In mid Jan 1999, half the saplings were decapitated, whereas the others remained intact. Controls remained in natural daylength and daylength was extended for experimental plants to ~13 h. Six weeks later, terminal buds of all intact treated plants had resumed shoot growth and formed several large leaves, whereas a few very small leaves just started appearing in the controls (Figure 6 B, C). In contrast, single, small shoots of similar size had developed from the uppermost lateral buds of decapitated plants in controls and treated plants alike (Figure 6 B).

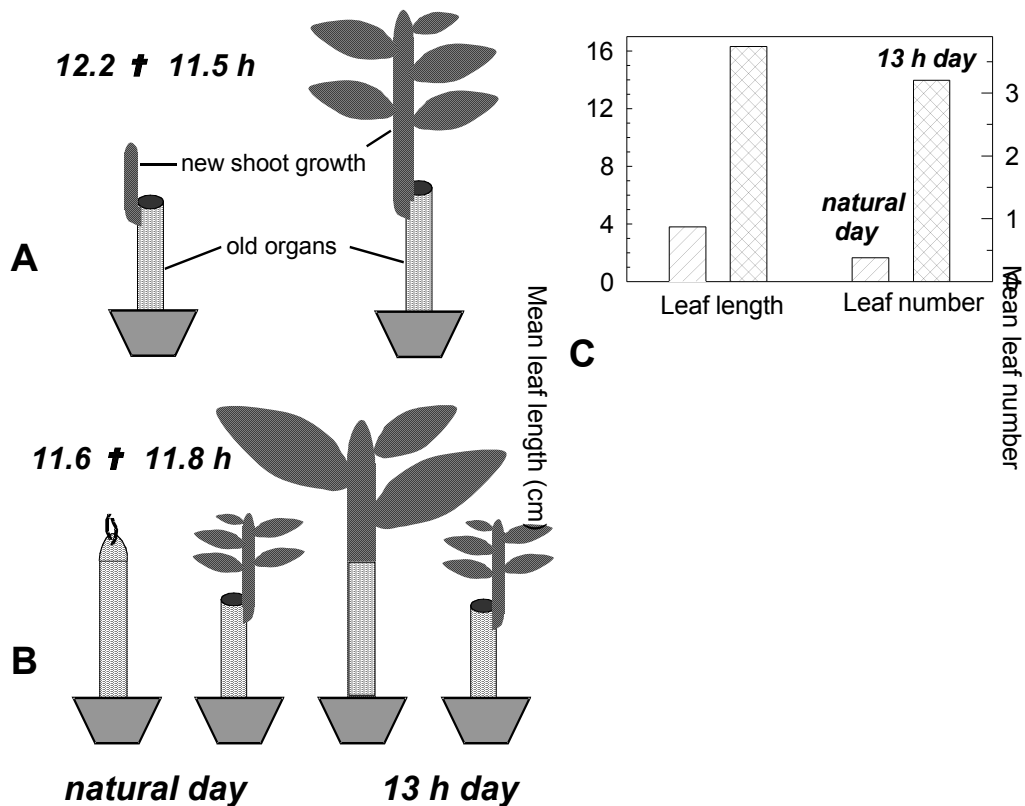


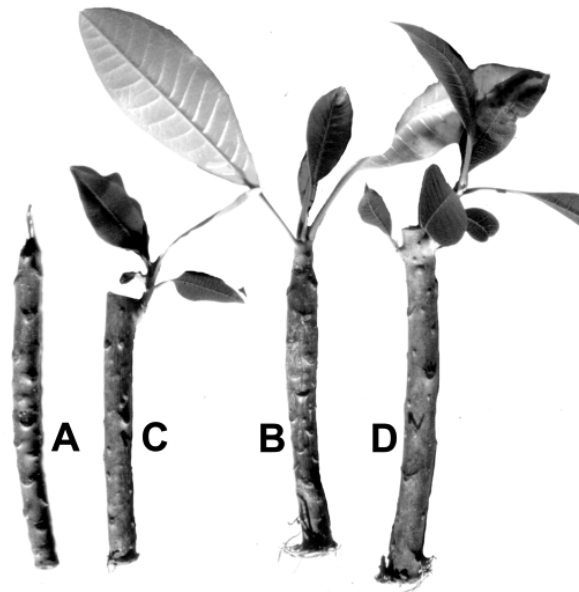
Figure 6. Effect of experimental daylight extension on shoot growth in saplings and cuttings of *Plumeria* observed in Cañas, Guanacaste, Costa Rica. A – Growth of lateral shoots from decapitated saplings during a decline in natural daylength from ~ 12.2 to 11.5 h (Aug.15 – Dec. 15). *Light hatching*: initial status of experimental plants; *dark hatching*: shoot growth during experiment. Left: growth under natural daylength. Right: growth under experimental 13-h photoperiod. B – Growth of terminal shoots on intact saplings and of lateral shoots on decapitated saplings under natural daylength of ~ 11.6 – 11.8 h (Jan. 15 – Feb. 25). C – Increase in mean leaf length (left) and leaf number (right) on terminal shoots of plants in B. *Diagonal hatching*: natural daylength; *cross-hatching*: extended daylength of ~ 13 h.

In a parallel experiment, the leafless, dormant, 30-40 cm long stems obtained from decapitated saplings (see above) were cut into an apical half with a terminal bud and a lower half (Figure 7). Cuttings were treated like the above saplings. After six weeks, shoot growth was identical to that in potted saplings, except that new shoots and leaves were much smaller. Also, in cuttings without an apical bud new lateral shoots in the controls were distinctly smaller than in the treated cuttings (Figure 7 C, D). In addition to new shoots, cuttings in daylight extension formed adventitious roots at their base and a ring of callus covering the exposed vascular tissues on the lower cut (Figure 7 B, D).

Photoperiodic control of shoot growth in Hildegardia barteri (Mast.) Kosterm.

In natural daylength, shoot and leaf growth of saplings of the West African stem succulent *Hildegardia* remain arrested between late Oct and Mar in Ibadan, Nigeria. Beginning in July, one-year-old saplings (~ 50 cm tall) were exposed to different photoperiods to study the effect of daylength on the induction of dormancy (Njoku 1964). In plants exposed to a 11.5 h photoperiod, shoot and leaf growth were arrested within 3 wk after the beginning of the experiment. Natural

Figure 7. Effect of extending daylength on shoot growth of 12-16 cm long cuttings of *Plumeria* with (A,B) and without (C,D) an apical meristem. A,C – natural daylength ~11.6 -11.8 h; B, D – experimental 13-h photoperiod. These cuttings formed many adventitious roots near their base (arrow) and a ring of callus tissues covering the exposed vascular tissues at the lower cut (not seen).



daylight and 12-h photoperiods induced dormancy by mid-Oct, but shoot growth was continuous in plants maintained in a 12.5 h photoperiod.

Conclusions

Experiments with *Plumeria* and *Hildegardia* confirm the conclusions drawn from phenological field observations. The decline in daylength to <12 h after the autumn equinox induced the arrest of growing apical meristems, which was prevented by extending daylength to 12.5 or 13 h. Night interruption as well as daylight extension to 13 h induced bud break in dormant terminal buds of intact trees, potted saplings and cuttings. Formation of lateral shoots in decapitated saplings and cuttings maintained under short photoperiods indicates that lateral buds are not dormant.

Does declining photoperiod cause leaf abscission?

In most stem-succulent trees, well hydrated leaves senesce and abscise rapidly during the early dry season. In potted, watered *Hildegardia* and *Plumeria* seedlings 3 –4 mo-old leaves abscised soon after the autumn equinox (see above) and declining photoperiods induce leaf senescence in some herbaceous species (e.g. soybean; Thomas and Vince-Prue 1997). Leaf abscission in stem succulents thus appears to be induced by declining photoperiod (Murashige 1966). However, several observations do not agree with this assumption. In Guanacaste, Costa Rica, leaves of large *Bombacopsis*, *Bursera* and *Plumeria* are consistently shed earlier than those of young trees or vigorous sprouts on heavily pruned trees in living fences. Similarly, along steep slopes trees at dry up-hill sites always shed leaves earlier than trees growing at the moister valley bottom. In natural daylength, leaves of trees and potted saplings of *Plumeria* gradually abscised from November to January (Figure 5; Murashige 1966, Lawton and Akbar 1968,). In trees exposed to experimental night interruption, leaf number declined slowly in Nov/Dec and started increasing in Jan, when new leaves expanded on new shoots. Gradual rather than synchronous leaf abscission and the effect of microsite water availability and tree size on leaf shedding suggest that in saplings and trees increasing leaf age and water stress rather than declining photoperiod are the principal causes of leaf shedding,

as they are in other tropical trees (Borchert 2000, Borchert et al. submitted). Periodic leaf shedding of *Bombax* in the humid, aseasonal climate of Singapore supports this view (Figure 5).

Discussion

Endo-dormancy of buds and its photoperiodic control distinguish stem succulents from other functional types of tropical trees (Borchert 2000, Borchert et al. submitted). Bud dormancy has been analyzed almost exclusively in temperate perennial plants, in which it is controlled by complex interactions between seasonal variation in temperature and daylength. In conjunction with cold hardiness, endo-dormancy of buds constitutes one of the principal physiological adaptations to seasonal climates with a cold winter (Borchert 1991, Crabbé and Barnola 1996, Thomas and Vince-Prue 1997). Photoperiodic control of shoot growth has been studied experimentally in seedlings and saplings of many temperate and a few tropical woody species (Romberger 1968, Longman 1978, Thomas and Vince-Prue 1997). Generally, short photoperiods slow down or arrest growth, whereas long photoperiods enable continuous shoot growth or induce bud break. In all these studies, the effect of large variations in photoperiod (8 –24 h light day⁻¹) on shoot growth was analyzed. The relevance of such experiments for tropical trees exposed to annual variation in daylength of < 1 h appears therefore questionable. In contrast to recent advances in the analysis of the molecular biology of biological clocks (Barinaga 1998), over the last 40 years there has been little, if any, progress in elucidating the cellular mechanisms controlling bud dormancy (Romberger 1968, Borchert 1991, Thomas and Vince-Prue 1997).

Shoot growth patterns of tropical stem succulents reveal basic aspects of the organismic control of bud dormancy, which are masked in temperate woody plants by the effects of seasonal variation in temperature and photoperiod. The vegetative phenology of *Bombax* observed near the equator in an aseasonal climate (Figure 4) indicates that shoot growth periodicity and bud dormancy are endogenous phenomena. As in all trees, rapid leaf expansion during flushing results in the arrest of shoot growth by correlative inhibition (Romberger 1968, Borchert 1991, 2000). The time of leaf abscission – and hence elimination of correlative bud inhibition by old leaves - is mainly determined by the species-specific life span of leaves, as it is in other tropical trees in humid climates (Borchert 2000, Borchert et al. submitted). The physiological causes for the unique persistence of bud dormancy after leaf fall and the delayed bud break several months after leaf shedding are entirely unknown.

Away from the equator, the endogenous shoot growth periodicity of *Bombax* is entrained to seasonal climate by annual variation in daylength. At low latitudes (7° N and S), where annual variation of photoperiod is less than 50 min, synchronous bud break of *Bombax* occurs soon after the spring equinox, i.e., an increase in daylength of <25 min is sufficient to break bud dormancy. In our experiments with *Plumeria* maintaining plants under 13-h photoperiods was sufficient to prevent the arrest of shoot growth by declining photoperiod (Figure 6 A) and to induce bud break of dormant shoots (Figs. 6 B; 7).

Several observations show complex, hard to explain interactions between positional and photoperiodic control of bud growth, for which there are no comparable observations for temperate trees (Romberger 1968). Endo-dormancy induced and broken by declining and increasing photoperiods, respectively (Figs. 5-7), appears to be limited to terminal buds. In *Plumeria* the elimination of apical dominance by decapitation induces bud break in the uppermost lateral buds irrespective of photoperiod (Figure 6 B, 7). In many Bombacaceae the elimination of correlative inhibition by abscission of old leaves triggers the gradual expansion of lateral flower buds (Figure 1 D, Jan/Feb). Inversely, formation of the lateral inflorescence normally associated with bud break of

Plumeria (Figure 3) remains suppressed during induction of bud break by night interruption (Figure 5; Lawton and Akbar 1968). Cuttings of *Plumeria*, which can be easily prepared in large numbers, should constitute a convenient experimental system for the future analysis of photoperiodic control of bud endo-dormancy.

Formation of adventitious roots and callus is likely to be induced indirectly by growth regulators diffusing down from the growing shoot, not directly by photoperiodic induction. Accordingly, a few adventitious roots developed in the decapitated controls with a small lateral shoot, but not in cuttings with a dormant apical bud (Figure 7 A, C). Similarly, in *Bombax ceiba* cell division in the cambium ceased in Nov and swelling of cambial cells started in Feb concurrent with the expansion of floral buds prior to anthesis (Rao et al 1996).

Adaptive value of endo-dormancy in tropical stem succulents

In addition to the capacity of storing large amounts of water, stem-succulents have evolved shoot growth patterns that minimize loss of stored water during the dry season and thus enable trees to survive long drought periods at very dry sites. The relatively short life span of leaves assures that rapid leaf abscission during early drought minimizes transpirational water loss by old leaves. Endo-dormancy of vegetative buds is induced by declining photoperiods after the autumn equinox which signal the end of the rainy season (Figure 1 A). This prevents water loss associated with the formation of short-lived leaf flushes in response to occasional rain-showers during the dry season (Bullock and Solis-Magallanes 1990, Borchert et al. submitted). Bud break is induced after the spring equinox by increasing daylength, which signals the approach of the wet season. In conjunction with the suppression of shoot and leaf expansion by low soil water content, this control mechanism assures that new shoots develop when soil water content is adequate to support shoot expansion (Figure 2) but not if drought persists (Bullock and Solis-Magallanes 1990).

Large cuttings of tropical stem succulent trees are widely used to establish tree rows for living fences (Jolin and Torquebiau 1992). Farmers in Costa Rica and other tropical countries have empirically established a planting schedule making optimum use of photoperiodic induction of bud break and the resulting formation of adventitious roots. Crown suckers (2-3 m long) are cut in March, stored upright for 3-4 weeks to allow healing of the basal cut and planted 50 cm deep in April, shortly before adventitious roots appear and the first rains moisten the top soil.

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