

Organismic and Environmental Controls of Bud Growth in Tropical Trees*

7

Rolf Borchert

Division of Biological Sciences, Haworth Hall, University of Kansas, Lawrence, KS 66045-2106, USA

Introduction

Periodic rather than continuous growth is almost universal among trees. In tropical as in temperate trees periods of shoot growth (flushing) alternate with periods of bud rest or dormancy. Various types of dormancy have been identified in woody plants adapted to temperate climates with a relatively short growing season and large annual variations in temperature and photoperiod which strongly synchronize vegetative and reproductive tree development (Fig. 7.1A; Crabbé, 1994: Table 1; Crabbé and Barnola, 1996: Fig. 6.1). In the tropics monthly mean temperatures often vary by $< 1-2^{\circ}\text{C}$ and annual variation in photoperiod is 1 h or less (Fig. 7.2). Climatic seasonality is therefore mainly determined by duration and severity of the dry season. For example, in the semideciduous tropical forest of Guanacaste, Costa Rica, where most research to be discussed here was done, less than 5% of annual precipitation normally falls during the 5–6 month-long dry season (Fig. 7.2).

In contrast with winter cold, severe seasonal drought does not strongly synchronize periodic development of tropical trees, and bud break in vegetative or flower buds during the dry season is common (Fig. 7.1B). Periodic tree development is even less synchronized in tropical forests with a short

* Dedicated to the memory of Charles Coster (1895–1943), last Dutch Director of the Buitenzorg Botanical Garden in Java. His pioneering studies of growth periodicity, dormancy and girth growth in tropical trees, published more than 70 years ago, address many of the questions discussed in this paper.

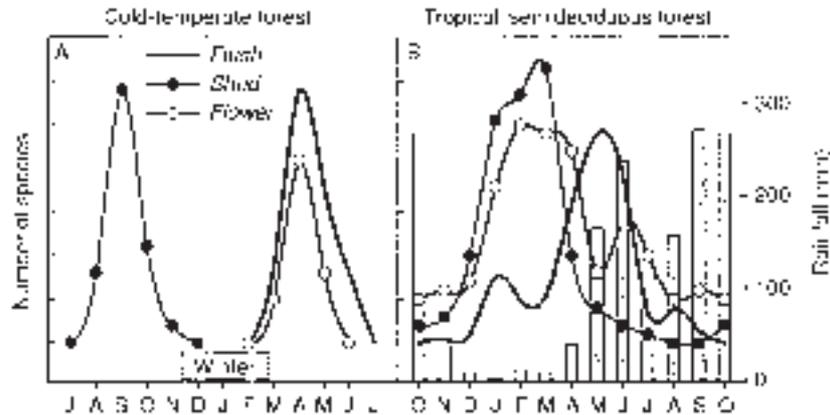


Fig. 7.1. Seasonal development (phenology) of broadleaved trees in a cold-temperate forest (A) and in a tropical semideciduous forest with a long, severe dry season (B; Guanacaste, Costa Rica). The sequence of months on the x-axis was chosen such that periods of climatic stress coincide in both graphs. Redrawn from Borchert (1998).

dry season (Borchert, 1998). The periodic arrest of shoot growth in such forests should be caused mainly by developmental constraints inherent in trees as large, complex, long-lived plants, not by environmental cues (Borchert, 1991, 1992; Crabbé and Barnola, 1996). These endogenous constraints are the consequence of size- and time-dependent changes in the functional interactions among a tree's organs and will be referred to as *correlative control*. With increasing climatic seasonality, the role of environmental changes causing the temporary arrest of bud growth become more important (e.g. control of bud dormancy of cold-temperate trees by annual variation in temperature and photoperiod). The progression from correlative to environmental control of bud growth in tropical trees will be discussed here.

Functional Tree Types in Tropical Dry Forests

In analogy to the synchronization of shoot growth periodicity by low winter temperatures (Fig. 7.1A), one might expect tropical forests with a long, severe dry season to be dominated by deciduous trees which shed leaves during the early dry season and resume growth after the first rains of the wet season (Fig. 7.2A; Fig. 7.3B,C). Instead, tropical dry forests constitute a mosaic composed of several functional tree types adapted to seasonal drought in different ways (Borchert, 1994a,b; Borchert and Rivera, unpublished). Of the functional tree types to be described here (Fig. 7.3), only *deciduous species* tolerate desiccation to very low water potentials (Fig. 7.4). Deep-rooted *evergreen* and *brevideciduous species* avoid severe water stress

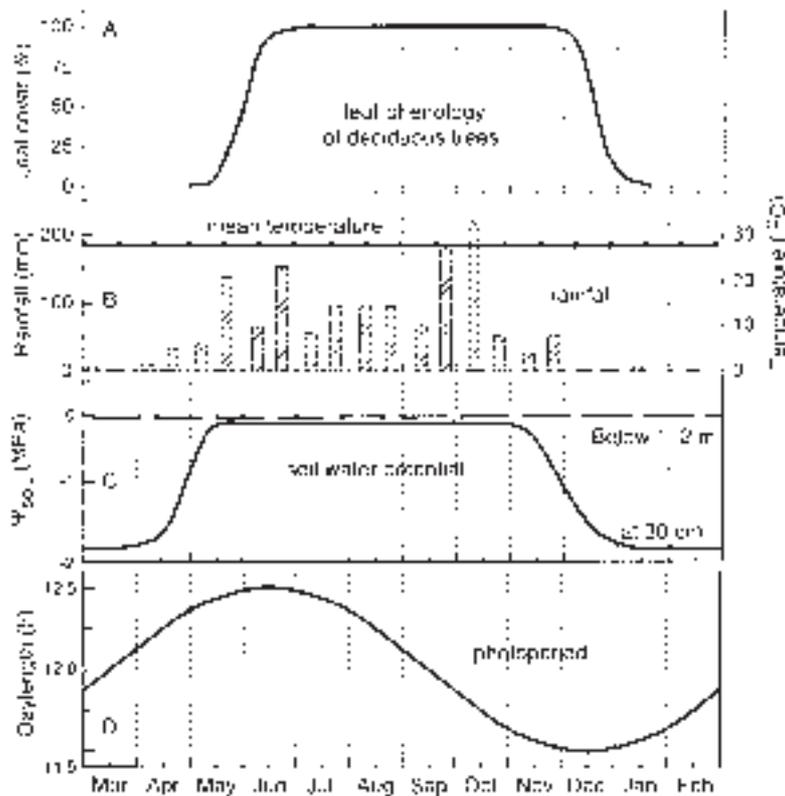


Fig. 7.2. Leaf phenology of deciduous trees (A), annual variation in rainfall and temperature (B), soil water potential (C) and photoperiod (D) in a tropical semideciduous forest in Guanacaste, Costa Rica.

during the dry season by extracting water from the moist subsoil (Fig. 7.2C), and *deciduous stem succulents* store large amounts of water in their stem tissues. Availability of stored water during climatic drought enables growth of vegetative and flower buds during the dry season and results in a large variety of species-specific patterns of bud growth (Fig. 7.3; Borchert, 1994a). Whereas the control of flower bud growth has received little attention in studies of dormancy in temperate trees, analysis of the large variety of flowering patterns (Fig. 7.3, F1–F12) is crucial to understanding the control of bud growth in tropical trees.

Deciduous species

Deciduous species have mesic leaves and often a shallow root system. As the topsoil dries out during the early dry season (Fig. 7.2, Dec), leaf and stem water potentials decline to very low values and leaves abscise (Fig. 7.4A).

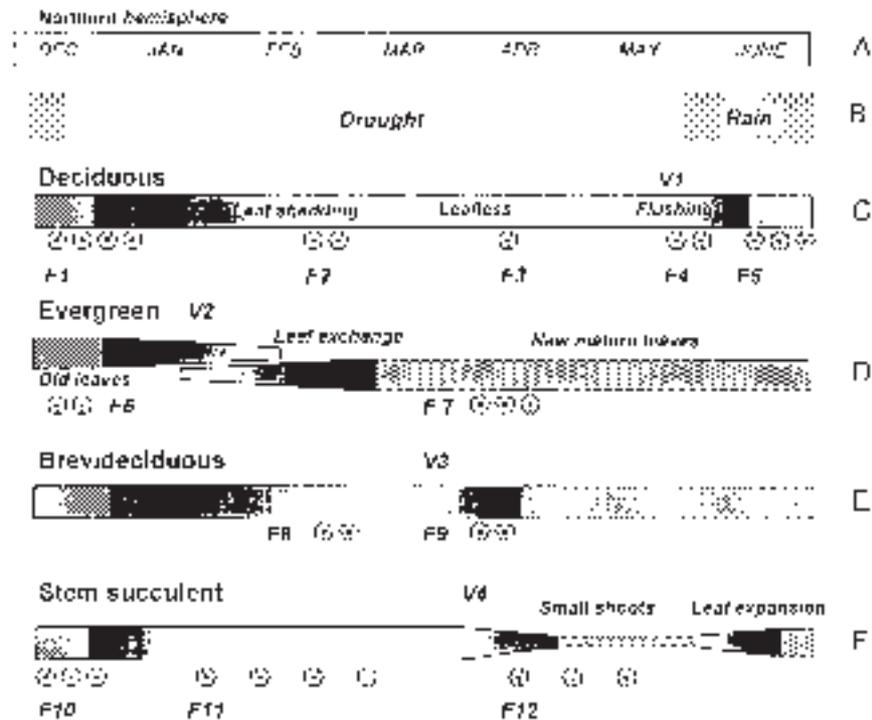


Fig. 7.3. Vegetative phenology (bars) and flowering episodes (⊗) in trees of four functional types (C–F) as observed during the dry season (A, B) in a semideciduous tropical forest in Guanacaste, Costa Rica. V1–V4, bud break of vegetative buds; F1–F12, bud break of preformed flower buds or appearance of terminal inflorescences. Causes of bud break discussed in the text: rain, V1, F3, F4; declining photoperiod, F1, F6, F10; increasing photoperiod, V3, V4, F12; leaf shedding, V2, F2, F8, F11; flowering on new shoots without identifiable cause, F5, F7, F9.

Bud break of vegetative buds occurs after the first rains have resaturated the topsoil (Fig. 7.2, May–June; Fig. 7.3, V1). At moist sites, deciduous species may exchange leaves during the dry season, i.e. they become evergreen. Flowering times vary widely, both between and within species. Preformed, resting flower buds open during the dry season at various times after leaf shedding (Fig. 7.3, F2, F3) or during bud break in vegetative buds (Fig. 7.3, F4). Flowers expand in the axils of leaves on new shoots (Fig. 7.3, F5) or apical meristems are transformed into terminal inflorescences during the mid- or late wet season (Fig. 7.3, F1).

Evergreen species

Evergreen species have long-lived, coriaceous leaves and deep roots. They are confined to microsites with subsoil water reserves and maintain

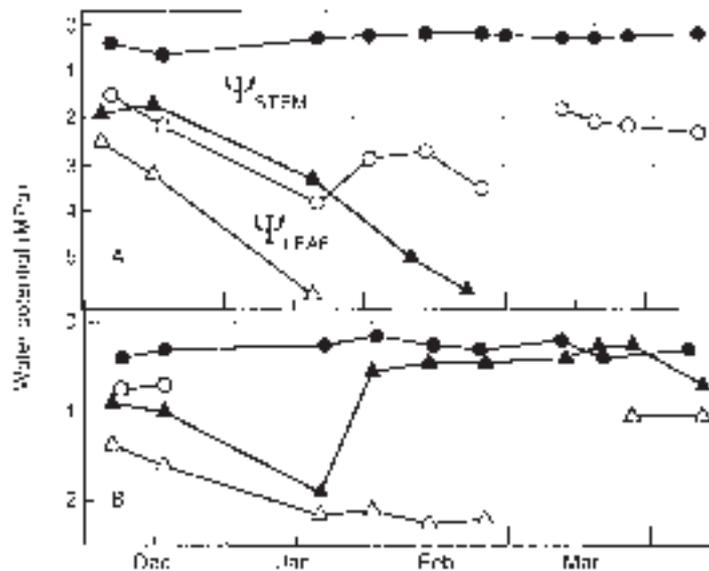


Fig. 7.4. Changes in predawn stem water potential (Ψ_{STEM} ; filled symbols) and midday leaf water potential (Ψ_{LEAF} ; empty symbols) associated with dry-season leaf phenology in trees of four functional groups. Gaps in Ψ_{LEAF} -values indicate that trees are leafless. A, evergreen (*Hymenea courbaril*; circles); deciduous (*Tabebuia ochracea*; triangles). B, brevideciduous (*Dalbergia retusa*; triangles); deciduous stem succulent (*Bombacopsis quinata*; circles).

relatively high stem water potentials throughout the year (Fig. 7.4A). Bud break of vegetative buds normally occurs during the early or mid-dry season shortly before or immediately after the completion of leaf shedding, i.e. trees 'exchange leaves' (Fig. 7.3D, V2; Longman and Jenik, 1988). Shoot growth often ends with the formation of a terminal inflorescence 1–2 months after flushing (Fig. 7.3D, F7).

Brevideciduous species

Brevideciduous (lat. *brevis* = short) species are similar in habit, distribution and water relations to evergreen species. However, synchronous bud break of vegetative buds generally occurs after mid-March and is preceded by a period of deciduousness which varies with the timing of leaf fall from several weeks to a few days (Figs. 7.3E, V3; Fig. 7.4B; Borchert *et al.*, unpublished). In some species preformed lateral flower buds expand when trees are leafless (Fig. 7.3E, F8), in others axillary flowers form on new shoots (Fig. 7.3E, F9).

Deciduous stem succulent species

Deciduous stem succulents have shallow root systems and mesic leaves, which are shed soon after the end of the wet season (Fig. 7.3F). Well adapted to very dry sites, succulent trees store large amounts of water in their trunks and maintain high stem water potentials throughout the dry season (Fig. 7.4B; Borchert, 1994b). In some species flushing is induced by the first heavy rains, in others bud break occurs during the late dry season, but stem elongation and leaf expansion are delayed until the first heavy rains resaturate the top soil (Fig. 7.3F, V4; Bullock and Solis-Magallanes, 1990). Trees flower at various times during the dry season (Fig. 7.3F, F10–F12).

Analysis of Bud Growth Patterns

Growth patterns discussed here were observed between 1991 and 1999 under normal climatic conditions (Figs 7.2 and 7.5) and as modified by large-scale natural experiments (Fig. 7.6: abnormal drought induced by the 1997 El Niño episode, abnormal dry-season rainfall in 1999) or irrigation (Fig. 7.6B; Borchert, 1994a,c; Borchert and Rivera, unpublished). Control mechanisms involved in bud break or growth arrest are inferred from temporal correlations between changes in environmental conditions, tree development and tree water status. Synchronous bud break of many trees in a landscape indicates an inductive environmental change such as rainfall or change in photoperiod. Correlative control is indicated by asynchronous bud break among conspecific trees in the absence of notable environmental change.

Changes in tree water status and soil water availability correlated with the initiation or arrest of bud growth were measured with a pressure chamber. Predawn stem water potential (Ψ_{STEM}) measured in defoliated twigs indicates the water status of tree branches at equilibrium with available soil water. The difference between Ψ_{STEM} and midday leaf water potential (Ψ_{LEAF}) reflects the balance between transpiration and water uptake and is an indirect measure of stomatal control (Borchert, 1994b; Borchert and Rivera, unpublished).

Correlative Control of Bud Growth

Correlative control of bud growth reflects functional interactions among the organs of a tree. Continuous shoot growth requires the provision of water, nutrients and growth regulators by other organs at rates exceeding consumption by growing shoots. As a tree increases in size and hence in the number of growing shoots and transpiring leaves, maintaining this

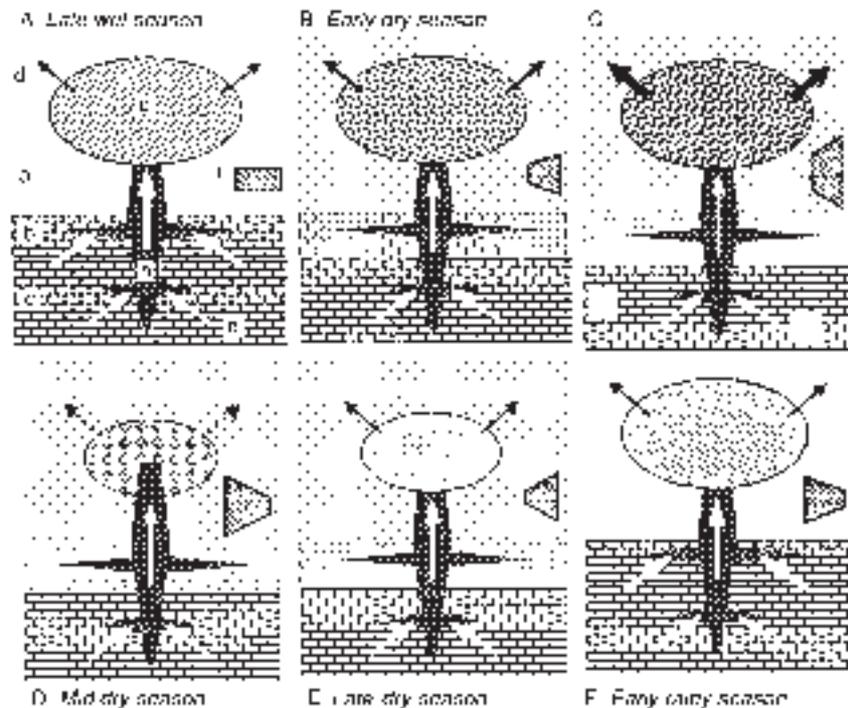


Fig. 7.5. Environmental and organismic changes resulting in leaf exchange of tropical trees during the dry season and in a second flush during the rainy season (schematic). A, Late rainy season: relative humidity (a) high; water content of topsoil (b) and subsoil (c) high; transpiration (d) low; water absorption (e) high; water stress (f) low [$\Psi_{\text{STEM}} > -1$ MPa]. B, Early dry season: relative humidity decreases; topsoil is drying out; transpiration increases; water stress increases. C, Several weeks after the last rain: topsoil is dry; water absorption is limited to deep roots (h) in moist subsoil; water stress enhances leaf senescence (g); transpiration by senescent leaves is very high; water stress becomes very high [$\Psi_{\text{STEM}} < -3$ MPa]. D, Abscission of senescent leaves: shedding of senescent leaves eliminates transpirational water loss; water absorption from subsoil continues; water stress becomes small [$\Psi_{\text{STEM}} > -0.5$ MPa]. E, Bud break and flushing: rehydration causes bud break; as leaves expand, transpiration increases; water stress increases and eventually arrests shoot growth. F, Early rainy season: relative humidity increases; top soil becomes water saturated; water absorption increases; water stress becomes small; bud break in vegetative buds initiates a second flush.

functional equilibrium becomes progressively more difficult (Borchert, 1991). In large, cold-temperate trees shoot growth therefore ceases well before the end of the growing season under climatic conditions permitting the continuing growth of tree saplings and herbs. Shoot growth may be arrested in the *absence* of adverse environmental conditions by a shortage in any one of the substances provided by other organs, i.e. by loss of the functional equilibrium among the tree's organs (Borchert, 1991; Crabbé

and Barnola, 1996). Correlative control of tree growth periodicity should be carefully distinguished from *spatial controls* such as apical dominance, which determine tree architecture and will not be discussed here. As the physiological mechanisms of correlative and spatial control differ substantially, applying the same term, paradormancy, to both mechanisms appears questionable (Lang *et al.*, 1987; Crabbé, 1994).

Defoliation soon after the end of seasonal shoot growth induces bud break and flushing in temperate trees (Borchert, 1991; Crabbé and Barnola, 1996). This indicates that trees have a limited carrying capacity for leaves and attain an optimum leaf area during each growing season. Leaves are involved in the correlative feedback inhibition arresting shoot growth once this optimum has been attained. Changes in tree water balance play a central role in the correlative control of bud rest and bud break of tropical trees during the dry season, when water is the principal factor limiting tree growth (Borchert, 1991, 1992, 1994a,b).

Leaf exchange of tropical trees during the dry season

Periodic leaf exchange in evergreen trees raises several questions. First, what causes leaf exchange in trees of moist forests with moderate seasonal drought? Second, why does leaf exchange always occur during the dry season? Third, given that cell expansion is strongly inhibited by water stress, how is it possible that in semideciduous forests bud break and shoot growth of evergreen and brevideciduous trees take place during climatic drought (Fig. 7.3)? The following multi-step model of the environmental and organismic changes resulting in leaf exchange during the dry season (Fig. 7.5) provides answers to these questions.

At the end of the wet season, tree tissues and soil are nearly water-saturated and relative humidity is high (Fig. 7.5A). After the cessation of rainfall, water content of the topsoil and relative humidity of the atmosphere decline and the tree water balance becomes negative (Fig. 7.5B). The resulting water stress enhances ageing and senescence of leaves, which at that time are 8–11 months old and approaching the end of their normal life span. Reduced stomatal control of senescent leaves (Reich and Borchert, 1988) in conjunction with increased evaporative demand of the atmosphere results in high transpiration rates at a time when the topsoil has become dry and water absorption is confined to deep roots in the moist subsoil (Fig. 7.5C). The resulting increase in leaf water stress (Fig. 7.4, decline in Ψ_{LEAF}) causes abscission of senescent leaves and hence elimination of water loss by transpiration (Fig. 7.5D). Continuing absorption of subsoil water reduces tree water stress (Fig. 7.5D), and rehydration of trees (Ψ_{STEM} near 0) causes bud break in vegetative or flower buds (Fig. 7.3, V2, F2, F8; Fig. 7.5E; Borchert, 1994a,b). At the height of climatic drought, leaf shedding thus causes a

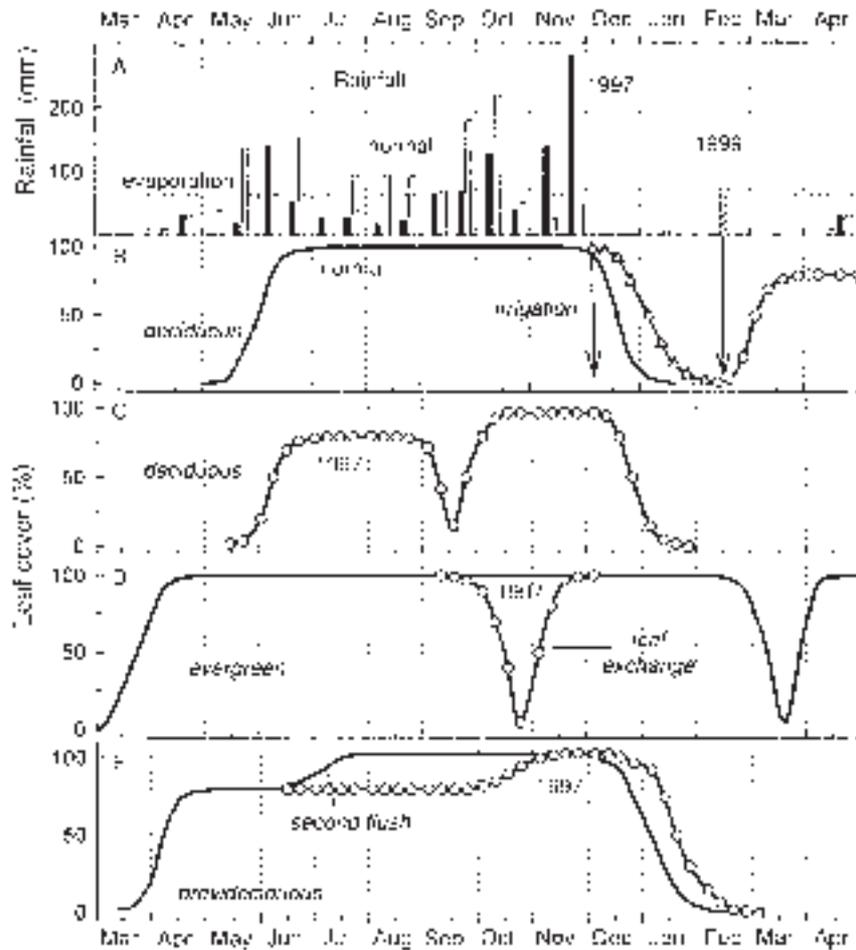


Fig. 7.6. Modification of seasonal development in a semideciduous forest of Costa Rica by abnormal drought or rain, and by irrigation. A, Normal rainfall (empty bars; mean 1991–1996), rainfall in 1997 (filled bars) and abnormal dry season rain in 1999 (crosshatched bar, Feb). B, Normal leaf phenology of deciduous trees (continuous line), delayed leaf abscission after irrigation (Dec–Jan; triangles) and flushing of leafless trees after rain during the dry season (Feb–Mar; circles). C, D, Abnormal leaf exchange caused by 1997 drought in deciduous (C) and evergreen species (D). E, Delayed second flush of brevideciduous species caused by 1997 drought.

dramatic shift in the functional relations between the root and shoot system, which results in rehydration and bud break. Shedding of senescent leaves, not environmental change, thus constitutes the indirect trigger of bud break (Borchert, 1992). The tight temporal correlation between leaf abscission and bud break of tropical evergreen and semideciduous trees has been described in several studies of tropical tree phenology, most

recently for trees of a tropical savanna in northern Australia (Williams *et al.*, 1997).

Quantitative differences in the driving variables of the model may cause large variations in the timing of leaf exchange and flowering. Generally, at moist microsites rehydration after leaf shedding is faster and the interval between leaf fall and bud break is shorter than at relatively dry sites (Borchert, 1994a,b). Along an altitudinal gradient of increasing water stress during the dry season, the phenology of several species changes gradually from an evergreen to a deciduous pattern, because leaves abscise progressively earlier and bud break occurs later with increasing drought (Borchert, 1991: Fig. 10.8). The 1997 El Niño episode interrupted the normal wet season with a severe 10-week drought in June–August (Fig. 7.6A; Borchert and Rivera, unpublished). The resulting water stress caused precocious leaf abscission and an abnormal leaf exchange in deciduous and evergreen species (Fig. 7.6C,D). In contrast, the 1998/99 La Niña event brought lower than normal temperature and wind speeds during the early dry season and delayed soil drying, leaf abscission and leaf exchange by 1–2 months relative to years with severe drought.

In all trees, the periodicity of meristem activity is punctuated by the periodic replacement of leaves, and the duration of each cycle is determined primarily by leaf longevity. Thus, leaves with a life span of 11–12 months determine the annual leaf exchange of evergreen and brevideciduous trees, and some species with short-lived leaves regularly exchange leaves twice a year (Borchert, 1991: Fig. 10.8, *Erythrina*). The endogenous periodicity resulting from the finite life span of leaves can be secondarily entrained to climatic seasonality by drought-induced acceleration of leaf shedding or delay of bud break (Fig. 7.6).

Flowering after leaf shedding

In several deep-rooted deciduous species and deciduous stem succulents preformed flower buds open soon after leaf shedding and branch rehydration during the dry season (Fig. 7.3, F2, F11; Borchert, 1994a,b).

Asynchronous development within tree crowns

Many travellers to the tropics are surprised to see different stages of seasonal development displayed at the same time within the crown of large trees. The upper, leafless branches may be covered with flowers, while lower branches bear senescent leaves. In keeping with the above model (Fig. 7.5), this asynchronous development is likely to be caused by differences in water relations among parts of the crown. Leaves are often shed first in branches which experience the greatest water stress, namely those located on top of

the crown or facing south (Fig. 7.7A). If soil water reserves are adequate, leaf shedding may trigger flowering, and growth of vegetative buds may start soon after flower abscission (Fig. 7.7B–D; Borchert, 1991: Fig. 10.8, *Erythrina*). As this developmental sequence progresses in the upper branches, lower branches with late leaf abscission pass through earlier stages of the sequence until the whole crown is again covered with mature leaves.

Asynchronous development may even occur on the same branch. In several deciduous species (e.g. *Gliricidia sepium*, *Caesalpinia eriostachys*) each axillary flower bud is released from correlative inhibition as soon as the subtending leaf has abscised (Borchert, unpublished). The correlative inhibition exerted by each senescent leaf thus extends just to its axillary bud. Accordingly, some sections of an annual shoot may bear old leaves, while axillary flowers or inflorescences are expanding on others.

Correlative arrest of shoot growth

Flushing after leaf exchange during the dry season is generally arrested within 1–2 months after bud break (Fig. 7.5D,E). Many evergreen and brevideciduous species (e.g. *Anacardium excelsum*, *Cassia grandis*, *Samanea saman*) regularly flush again during the rainy season (Figs 7.5E and 7.6E, July). In 1997, this second flush was delayed in many trees by abnormal drought until rainfall increased in September (Fig. 7.6E, Oct). These observations indicate that shoot growth is arrested by water stress resulting from an increase in leaf area and transpiration during the dry season (Fig. 7.5E). Bud growth resumes once a positive water balance has been re-established during the wet season (Fig. 7.5F). Accordingly, early leaves formed during the dry season are generally smaller than later leaves expanding during the wet season (Fig. 7.8). In some species naked terminal buds are arrested by correlative inhibition and resume growth after the first rains, in others second flushes originate from resting lateral or terminal buds of the first

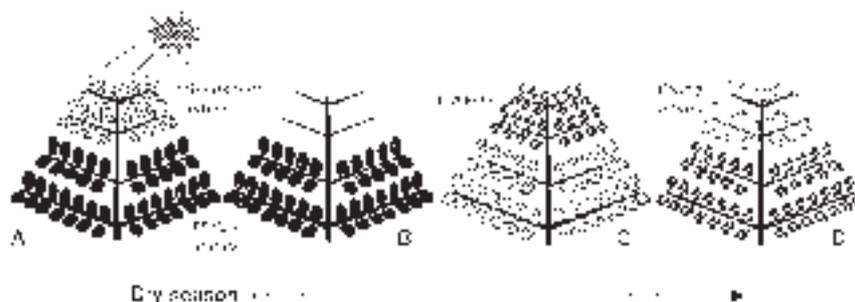


Fig. 7.7. Asynchronous dry season phenology within a tree crown (schematic). For explanation see text.



Fig. 7.8. Dry season and rainy season flushes. Left: second half of a long, continuous flush with larger leaves and axillary flower buds (*Diospyros nicaraguensis*). Right: second flush arising from an axillary bud below the terminal inflorescence on the first flush (*Godmania aesculifolia*; mature leaves cut off).

flush (Fig. 7.8). Similarly, resumption of root growth after transfer of pot-bound saplings to a larger container causes bud break in oak (Borchert, 1991). Any organismic or environmental change affecting tree water balance may thus cause the arrest or resumption of shoot growth.

Control of Bud Growth by Environmental Factors

Tropical rain forest trees tolerate neither cold nor severe drought (Borchert, 1998), but trees adapted to strongly seasonal climates have evolved tolerance of the climatic extremes of their habitat. In cold-temperate trees, buds in a state of dormancy imposed by low temperature (ecodormancy) resume growth as soon as temperature is raised to a permissive level. In autumn, complex, poorly understood interactions between declining temperature and photoperiod induce cold hardiness and endodormancy, during which buds are unable to grow even when transferred to favourable conditions (Borchert, 1991; Crabbé, 1994; Crabbé and Barnola, 1996).

Drought-imposed Ecodormancy in Deciduous Trees

During the dry season, irrigation or rainfall exceeding 20–30 mm induce rapid rehydration and expansion of preformed flower buds in deciduous trees of tropical dry forests in Central America and Mexico (Fig. 7.3, F3, F4;

Opler *et al.*, 1976; Reich and Borchert, 1982; Bullock, 1986; Borchert, 1994c). Irrigation or an exceptional 75-mm rainfall in mid-February 1999 caused rapid flushing in most leafless trees, scattered bud break on leafless twigs of leafy trees, and no bud break in trees with a full crown of old leaves (Fig. 7.6B; Borchert, 1994c; Borchert *et al.*, unpublished). Similarly, irrigation did not cause earlier than normal flushing in leaf-bearing evergreen and semideciduous trees in Panama and northern Australia (Wright and Cornejo, 1990; Myers *et al.*, 1998). Neither irrigation nor abnormal dry-season rain induced bud break in leafless stem succulent trees (e.g. *Bombacopsis*, *Bursera*, *Plumeria*; Borchert and Rivera, unpublished).

Elimination of water deficits in leafless trees by irrigation or rainfall during the dry season thus induces rapid flushing or flowering in many species. This indicates that bud rest during the dry season is generally imposed by water stress, i.e. resting buds are in a state of ecodormancy with low water potentials inhibiting bud growth. In contrast to the induction of cold hardiness in temperate trees by declining temperature and photoperiod, there is no evidence for a specific induction of drought tolerance, i.e. generally deciduous species are drought-tolerant and evergreen species are not. Irrigation or rain cannot overcome correlative inhibition of bud break by senescent leaves, which – as strong sinks for available water – are likely to inhibit rehydration of their axillary buds (Figs 7.4 and 7.5). Lack of bud break in leafless stem succulents with a high Ψ_{STEM} (Fig. 7.4B) indicates that buds are in a state of endodormancy similar to that of dormant temperate trees. In a pioneering study, Coster (1923) applied treatments known to break winter dormancy in temperate woody plants to cuttings of the stem succulent *Bombax malabaricum*. He was unable to break endodormancy at the height of the dry season, but achieved rapid bud break shortly before flushing of trees in the field.

Photoperiodic Control of Bud Growth

All instances of bud break discussed so far are preceded by environmental (rainfall, irrigation) or correlative changes (leaf abscission) which cause bud break by reducing water stress. This mechanism cannot explain the following examples of synchronous bud break not preceded by notable climatic or correlative changes. After several months of rest, lateral or terminal buds resume growth during the late rainy season and form inflorescences on leafy branches, i.e. they escape correlative bud inhibition by old leaves (Fig. 7.3, F1, F6, F10; Fig. 7.9B, Oct–Dec). In brevideciduous and stem succulent species vegetative buds expand during the late dry season, weeks before the first rains and rehydration of the top soil (Fig. 7.3, V3, V4; Fig. 7.9B, Mar–Apr; Borchert *et al.*, unpublished). In brevideciduous trees the rate of subsequent stem and leaf expansion varies widely with microsite water availability and in stem succulents shoot expansion is

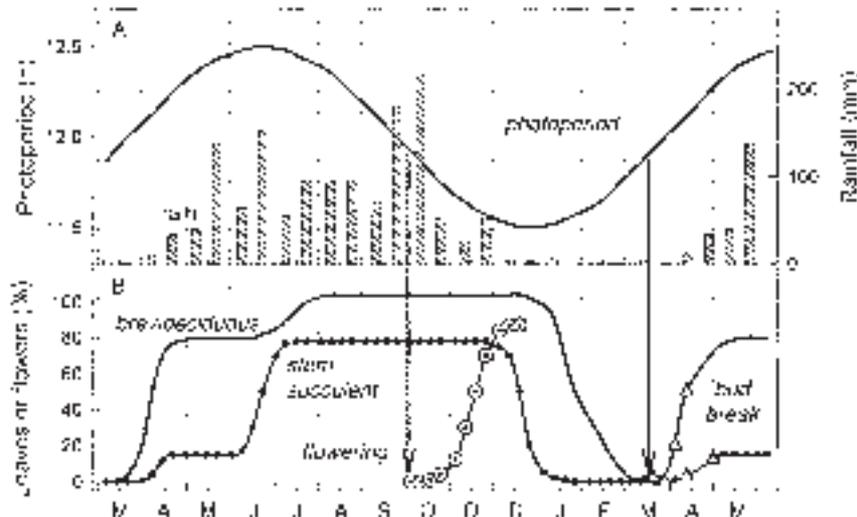


Fig. 7.9. Photoperiodic control of bud break (schematic). A, Seasonal variation in photoperiod and rainfall in Guanacaste, Costa Rica. B, Induction of flowering by declining photoperiod (Oct/Nov; dotted circles) and of bud break in brevideciduous and stem succulent species by increasing photoperiod (Mar–Apr; triangles).

delayed until after the first rains. Bud break always occurs within 1–2 weeks in all observed conspecific trees (Table 7.1). This distinct synchrony of flowering and bud break soon after the autumn and spring equinox, respectively, suggests that small changes in daylength constitute the environmental cue for bud break (Fig. 7.9; Thomas and Vince-Prue, 1997).

Experimental analysis of photoperiodic control of seasonal development is impractical in large trees. The following criteria were therefore established to screen field observations for potential photoperiodic induction of bud break. None of these criteria will prove photoperiodic control, but confirmation of several criteria in more than 20 tropical tree species provides strong indirect evidence for the control of flowering and bud break by small changes in daylength. Only a few representative observations made in 1997–1999 can be described here.

Synchrony and low inter-annual variation of bud break

Because of local variation in microsite water availability, patchiness of rainshowers, and inter-annual variation in climate, the timing of bud break induced by rehydration of twigs varies widely among conspecific trees (see section on correlative control). In contrast, bud break induced by changes in photoperiod should be synchronous throughout a landscape and occur each year at the same species-specific time.

Table 7.1. Representative trees and herbs with photoperiodic control of bud break in the semideciduous forest of Guanacaste, Costa Rica. Dates of first observation are given for short-day induced flower buds and for long-day induced bud break. N, number of observed trees. References: a, Borchert, 1996; b, Rivera and Borchert, unpublished; c, Borchert *et al.*, unpublished.

Date	Species	N	Figure	Reference
Short-day-induced flowering in herbs				
20–30 September	<i>Hyptis</i> and other herbs	> 50		b
20–30 September	<i>Hyparrhenia</i> and other grasses	> 50		b
Short-day-induced flowering in trees				
1–10 October	<i>Lonchocarpus minimiflorus</i>	> 50		b
10–20 October	<i>Bauhinia unguolata</i>	> 50		b
20–31 October	<i>Calicophyllum candidissimum</i>	> 50	7.10C	a, b
1–10 November	<i>Luehea speciosa</i>	> 30	7.10A	a, b
1–10 November	<i>Ochroma pyramidale</i>	> 20		b
20–30 November	<i>Cordia alliodora</i>	> 50	7.10B	a, b
20–30 November	<i>Cochlospermum vitifolium</i>	> 40		a, b
Long-day-induced bud break				
Brevideciduous trees				
20–30 March	<i>Cassia grandis</i>	> 30		a, c
20–30 March	<i>Dalbergia retusa</i>	> 40	7.11A	c
20–30 March	<i>Guazuma ulmifolium</i>	> 50	7.11B	a, c
Stem succulent trees				
10–20 March	<i>Plumeria rubra</i>	> 20	7.12	c
1–10 April	<i>Bursera simarouba</i>	> 40	7.11C	a, c
20–30 April	<i>Bombacopsis quinatum</i>	> 30		c

Between October and December, synchronous initiation of flower bud development was observed at a wide range of microsites and elevations in leafy shoots of several Costa Rican dry-forest species (Table 7.1; Rivera and Borchert, unpublished). In Mexico, more than 20 trees of four species flowered synchronously during September/October in 4 consecutive years (Bullock and Solis-Magallanes, 1990). Herbarium specimens collected over many years show flowering in such species to begin in September/October (Fig. 7.10; Borchert, 1996). Among Costa Rican trees and herbs, flower bud development induced by declining daylength started at different times between late September and December, indicating interspecific variation in critical daylength (Table 7.1).

Synchronous bud break of brevideciduous and stem succulent trees after mid-March was observed repeatedly in the semideciduous forest of Costa Rica (Fig. 7.11; Table 7.1). In a dry monsoon forest in Northern Thailand, sets of ten trees in several species flushed during the same month

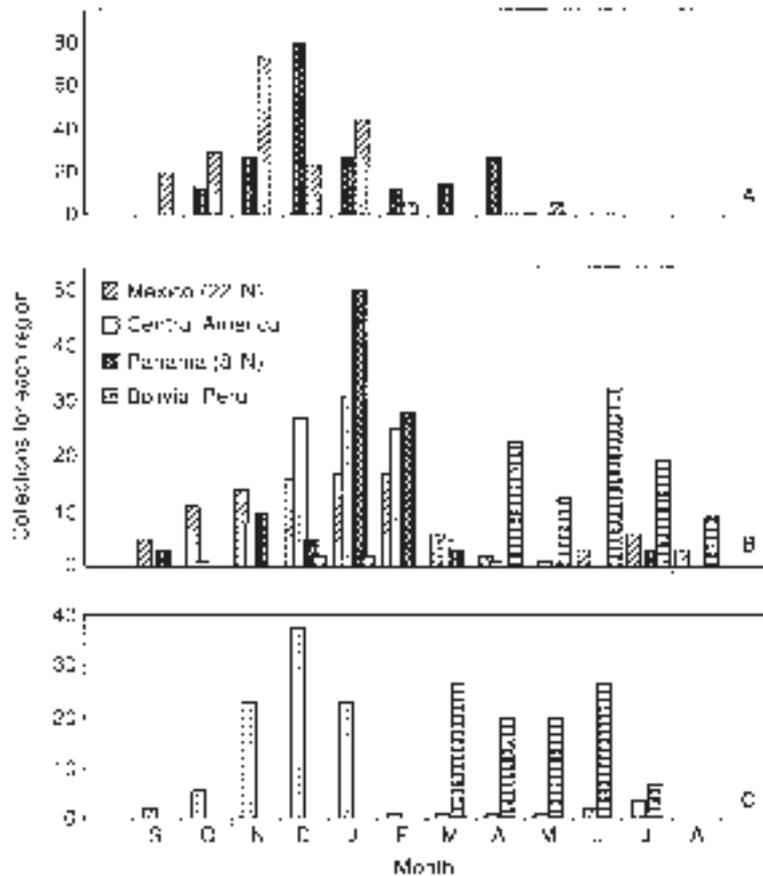


Fig. 7.10. Flowering induced by declining photoperiod in four species ranging from Mexico to South America. Flowering periodicity obtained from collection dates of herbarium specimens of the Missouri Botanical Garden, St Louis, USA (number of collections for each species in parentheses). A, *Luehea speciosa* (97); B, *Cordia alliodora* (401); C, *Calicophyllum candidissimum* from Central America (109; left) and *Calicophyllum multiflorum* from Bolivia and Peru (15; right).

in 3 consecutive years (Borchert *et al.* unpublished). Herbarium collections of species flowering on new shoots (Fig. 7.3, F9, F12) provide long-term evidence for bud break in March/April (Fig. 7.11, right; Borchert, 1996).

Time of bud break

Short-day induced flowering and long-day induced synchronous bud break was not observed before the equinoxes. This suggests that at low latitudes, where annual variation in daylength is 1 h or less, changes in photoperiod

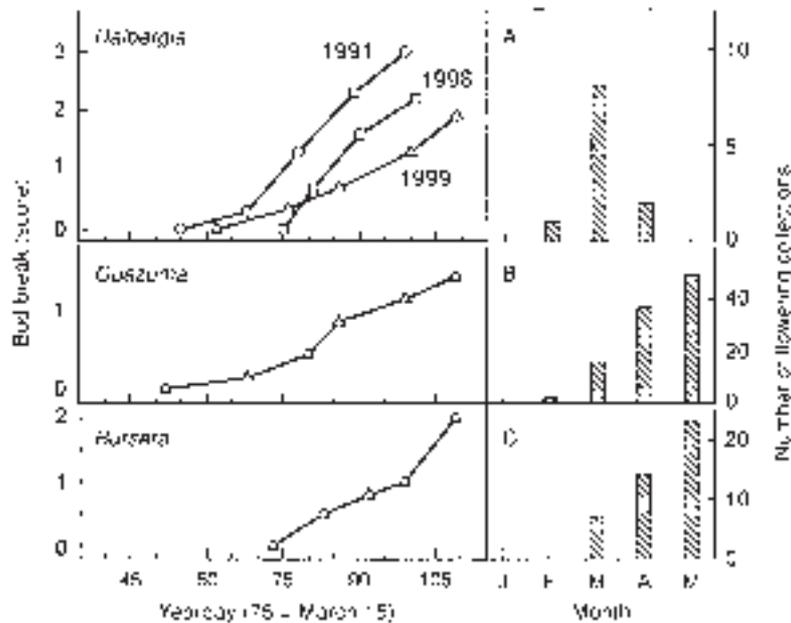


Fig. 7.11. Bud break induced by increasing photoperiod in two brevideciduous species (A, *Dalbergia retusa* (11); B, *Guazuma ulmifolia* (104) and a deciduous stem succulent (C, *Bursaria simarouba* (46)). Left: bud break in various years. Right: long-term periodicity of flowering on new shoots obtained from collection dates of herbarium collections (see Fig. 7.10).

sufficiently large to trigger bud break occur only around the spring and autumn equinox, when daylength change is fastest (Fig. 7.9A).

Variation of bud break with latitude

Within wide-ranging species or genera the timing of bud break should differ by 6 months between the Northern and Southern hemispheres, as observed for several widely distributed neotropical trees (Fig. 7.10B,C; Coster, 1923; Justiniano and Fredericksen, 2000). Such species flower year-round near the equator (Borchert, 1996: Figs 3F and 7J).

Short-day induced flowering starts about 1 month earlier in subtropical Mexico (20–23°N) than in tropical Panama and northern South America (5–8°N; Fig. 7.10A,B), and flowering in subtropical Bolivia (18°S) is 6 months out of phase with Mexico (Fig. 7.10C; Justiniano and Fredericksen, 2000). These observations suggest that the critical daylength for short-day flowering is slightly longer than 12 h in ecological races of the subtropics, where rainfall ceases earlier than at low latitudes. Variation in

critical daylength with latitude is well known for wide-ranging temperate tree species (Thomas and Vince-Prue, 1997).

Experimental extension of daylength

The effect of a 1.5 h daylength extension on flowering and bud break was studied in several Costa Rican herbs and tree saplings.

- *Suppression of short-day-induced flowering.* Flowering was suppressed by 1.5 h of supplementary light in several herbs and grasses flowering during the late rainy season (Table 7.1; Rivera and Borchert, unpublished).
- *Endodormancy in Plumeria.* Under natural daylength, the apical meristem of potted, watered saplings of the stem succulent *Plumeria rubra* remained dormant from September to early March, i.e. buds were in a state of endodormancy like those of *Bombax malabaricum* (Coster, 1923). Under natural daylength saplings decapitated in August had formed no shoots or very small shoots with a few leaves by December; if exposed to 1.5 h of supplementary light, plants formed shoots with large leaves (Fig. 7.12A). During a 6-week period beginning 15 January, apical cuttings stored moist in plastic bags remained dormant under natural daylength (Fig. 7.12B). If exposed to supplementary light, cuttings formed new shoots and, on the cut basal surface, callus and adventitious roots (Fig. 7.12C; Borchert and Rivera, unpublished). Thus, endodormancy of apical meristems in *Plumeria* was induced and maintained by photoperiods of <12 h, but broken by photoperiods of ~13 h.

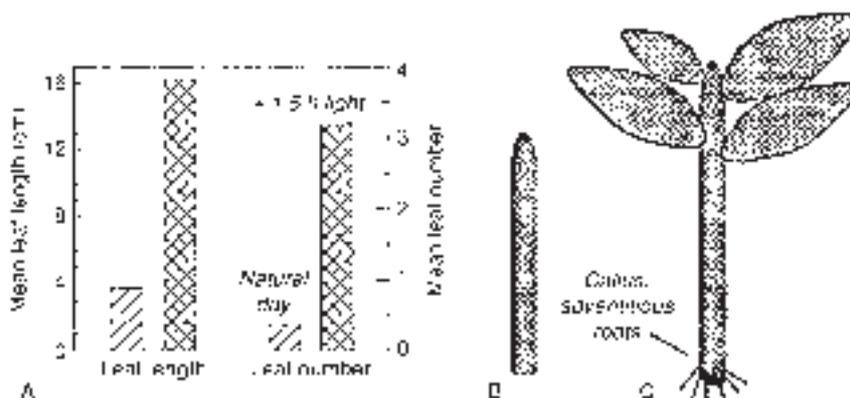


Fig. 7.12. Photoperiodic control of endodormancy in *Plumeria rubra*. Effect of 1.5 h supplementary light on leaf growth of decapitated saplings from August to December 1998 (A). Development of 20-cm-long cuttings from 15 January to 28 February, 1999 under natural daylength (B) or with 1.5 h daylight extension (C).

The combination of phenological field observations, herbarium collections and experimental results strongly supports the hypothesis that in tropical trees changes in photoperiod of < 30 min may control endodormancy and induce the transformation of vegetative into flowering meristems. Seasonal rainfall in the tropics is tightly linked with the zenithal position of the sun (Nieuwolt, 1977). Declining and increasing photoperiods thus indicate the imminent end of the rainy season and of seasonal drought, respectively (Fig. 7.9). Short-day induction of flowering is common in tropical herbs, which complete seed set before dying during seasonal drought (Ison and Hopkinson, 1985). It appears that with the exception of the woody short-day plant *Euphorbia pulcherrima* (Poinsettia), photoperiodic flower induction has not been reported for tropical or temperate trees. Stimulation of shoot and leaf growth of tropical and temperate trees by long photoperiods is well known, but the control of endodormancy by small variations in daylength has been described only once, for the African species *Hildegardia barteri* (Thomas and Vince-Prue, 1997).

Conclusions

Current concepts of types and mechanisms of bud dormancy in woody plants are based mainly on the analysis of seasonal development in cold-temperate species adapted to a climate which imposes a single pattern of vegetative and reproductive development on most broadleaved trees (Fig. 7.1A). Among tropical trees various patterns of periodic development have evolved in response to variation in the severity of seasonal drought (Fig. 7.3). Where seasonal water stress is moderate, tree growth periodicity is mainly the result of endogenous, correlative controls. The analysis of tropical trees therefore reveals characteristic aspects of correlative control, which are masked in temperate trees by the predominant role of environmental controls. Periodic replacement of leaves with a species-specific, finite life span constitutes the endogenous timer of shoot growth periodicity, and period length varies with leaf life span from 6 to 12 months. Bud break is caused mainly by changes in tree water relations resulting from leaf abscission (Fig. 7.5). Intra- and interspecific variation in the timing of bud break in vegetative or flower buds is large (Fig. 7.3).

Severe seasonal drought may entrain the endogenous growth periodicity of tropical trees to climatic seasonality by enhancing leaf abscission or delaying rehydration required for bud break (ecodormancy). Small changes in daylength may induce synchronous flowering or impose and release endodormancy in the absence of climatic change. The variety of seasonal growth patterns observed in tropical trees of different functional types (Fig. 7.3) reflects the predominance of different controls of bud growth. Spatial controls of tree architecture and correlative controls of periodic growth operate in all trees, but are supplemented in trees adapted

to seasonal water stress by eco- or endodormancy induced by environmental factors.

Acknowledgements

The Program of Terrestrial Ecology of the Andrew W. Mellon Foundation supported recent field research reported here. I thank Dr Missy Holbrook, Harvard University, Dr Craig Martin, University of Kansas and Dr Guillermo Rivera, Universidad de Cordoba, for critically reading the manuscript.

References

- Borchert, R. (1991) Growth periodicity and dormancy. In: Raghavendra, A.S. (ed.) *Physiology of Trees*. John Wiley & Sons, New York, pp. 221–245.
- Borchert, R. (1992) Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical forests. *Biotropica* 24, 385–395.
- 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) Water status and development of tropical trees during seasonal drought *Trees* 8, 115–125.
- Borchert, R. (1994c) 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. (1996) Phenology and flowering periodicity of neotropical dry forest species: evidence from herbarium collections. *Journal of Tropical Ecology* 12, 65–80.
- Borchert, R. (1998) Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change* 39, 381–393.
- Bullock, S.H. (1986) Observations and an experiment on synchronous flowering. *Madroño* 33, 223–226.
- Bullock, S.H. and Solis-Magallanes, J.A. (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22, 22–35.
- Coster, C. (1923) Lauberneuerung und andere periodische Lebensprozesse in dem trockenen Monsungebiet Ost-Javas. *Annales du Jardin Botanique Buitenzorg* 33, 117–189.
- Crabbé, J. (1994) Dormancy. In: *Encyclopedia of Agricultural Sciences*, vol 1. Academic Press, San Diego, pp. 597–611.
- Crabbé, J. and Barnola, P. (1996) A new conceptual approach to bud dormancy in woody plants. In: Lang, G.A. (ed.) *Plant Dormancy: Physiology, Biochemistry and Molecular Biology*. CAB International, Wallingford, UK, pp. 83–113.
- Ison, R.L. and Hopkinson, J.M. (1985) Pasture legumes and grasses in warm climate regions. In: Halevy, A.H. (ed.) *CRC Handbook of Flowering*. CRC Press, Boca Raton, Florida, pp. 203–251.
- Justiniano, M.J. and Fredericksen, T.S. (2000) Phenology of tree species in Bolivian dry forests. *Biotropica* (in press).

- Lang, G.A., Early, J.D., Martin, G.C. and Darnell, R.L. (1987) Endo-, para-, and eco-dormancy: physiological terminology and classification for dormancy research. *HortScience* 22, 371–377.
- Longman, K.A. and Jenik, J. (1988) *Tropical Forest and its Environment*. Longman, London.
- Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A. and Eamus, D. (1998) Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of Northern Australia? *Australian Journal of Ecology* 23, 329–339.
- Nieuwolt, S. (1977) *Tropical Climatology*. John Wiley & Sons, London.
- Opler, P.A., Frankie, G.W. and 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.
- Reich, P.B. and Borchert, R. (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 64, 294–299.
- Reich, P.B. and Borchert, R. (1988) Changes with leaf age in stomatal function and water status of several tropical tree species. *Biotropica* 20, 60–69.
- Thomas, B. and Vince-Prue, D. (1997) *Photoperiodism in Plants*. Academic Press, San Diego.
- Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A. and Eamus, D. (1997) Leaf phenology of woody species in a Northern Australian tropical savanna. *Ecology* 78, 2542–2558.
- Wright, S.J. and Cornejo, F.H. (1990) Seasonal drought and leaf fall in a tropical forest. *Ecology* 71, 1165–1175.

