

# 10 Growth Periodicity and Dormancy

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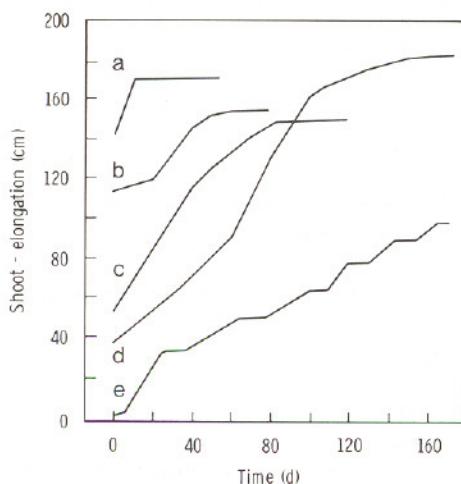
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## 10.1. Shoot growth in tropical and temperate trees

Periodic (or episodic, intermittent, rhythmic) rather than continuous growth is almost universal among trees (1,2). Periods of rapid shoot growth (*flushing*)

usually alternate with periods of rest. In seasonal climates, environmental control of growth periodicity is indicated by the synchronized bud break and flushing observed in deciduous temperate or tropical trees in response to favorable temperatures or the first heavy rains, respectively. However, unexpectedly, most mature trees complete a single, relatively short, annual period of shoot growth well before the end of the growing season, and growth remains arrested for the remainder of the year (Fig. 10.1).

Many young trees grow continuously for several months in favorable environments, but saplings of trees such as *Hevea* (rubber; Fig. 10.2C,D), *Theobroma* (cacao; Fig. 10.6 inset), *Quercus* (oak; Fig. 10.3) or *Pinus* (pine; Fig. 10.1e) pass through as many as 15 growth cycles per year (3–5). Periodic shoot growth under such conditions is asynchronous among the trees of a population (6), and, in the wet tropics, flushes of shoot growth may be asynchronous even within the crown of individual trees (2). The arrest of shoot growth and the duration of the rest period are therefore not determined by changes in environment, but must be regulated by physiological changes within the tree. Trees passing through repeated cycles of growth and rest unrelated to environmental changes thus manifest an endogenous growth periodicity, often referred to as *rhythmic growth* (Figs. 10.2C,D, 10.4).



**FIG. 10.1.** Patterns of seasonal shoot growth in 5–10-year-old temperate trees. (a) *Aesculus* (buckeye). (b) *Carya* (hickory): single flush of determinate shoot growth with expansion of the leaves (performed in the winter bud) followed by growth cessation and formation of a terminal bud early in the growing season. (c) *Fraxinus* (ash). (d) *Salix* (willow): indeterminate shoot growth during which newly initiated leaves expand during a prolonged growth period. (e) *Pinus palustris* (longleaf pine): recurrent flushes of determinate shoot growth with terminal bud formation at the end of each flush. (Redrawn from Refs. 1,11.)

### 10.1.1. *Tree growth periodicity: a new perspective*

Most research on tree growth has focused on the environmental control of periodicity and the mechanism of dormancy in a few temperate fruit and timber tree species. Consequently, all earlier discussions of tree growth periodicity have considered annual tree development including a period of winter dormancy as the normal situation, rather as a specific developmental pattern adapted to cold-temperate climates (7,8).

Our increased knowledge of growth patterns in tropical trees provides the opportunity to review tree development from a new, broader perspective. In a radical departure from the past, growth periodicity in trees will be considered here to be primarily an inherent consequence of the developmental constraints of trees as large, long-lived plants pursuing a characteristic adaptive strategy (Section 10.8).

Because of the present limited understanding of the causal factors responsible for the induction and breaking of rest periods in trees, too many terms have been coined in the past to describe different types of dormancy (9). To simplify matters, only two operationally defined "states" of apical meristems will be distinguished here: (a) *resting buds* or meristems, which resume growth within 1–2 weeks after being transferred to favorable growing conditions and (b) *dormant buds* or meristems, which do not resume growth within this time period. Unless exposed to a specific set of environmental conditions, such buds—like dormant seeds—may remain inactive even under favorable conditions for several weeks or months.

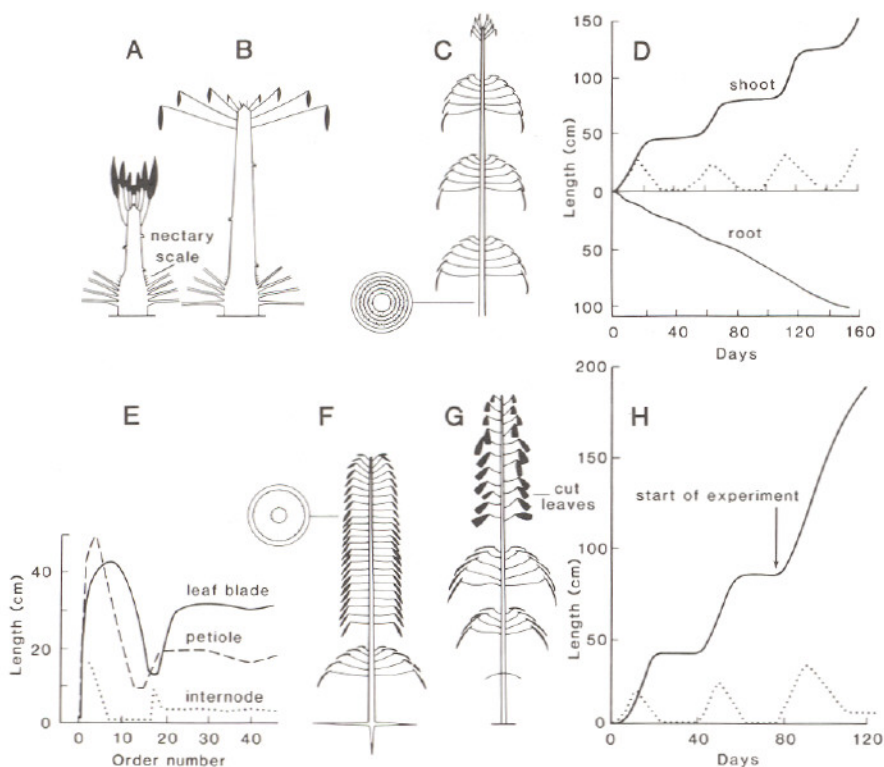
## 10.2. Shoot morphogenesis

Much of the current knowledge on periodic shoot growth has been gained not by measurements of extension growth (Figs. 10.1, 10.2D), but from phenological observations on the timing of bud break, leaf expansion, flowering, and leaf fall (Section 10.5), as well as from analyses of tree morphology. Because of the distinct morphogenetic changes usually associated with the onset and termination of shoot growth, stem sections formed during a period of shoot extension can be easily recognized. Morphology and architecture of a tree thus provide a lasting record of its developmental history (10).

### 10.2.1. *Periodic growth in Hevea*

The pattern of developmental changes occurring during one period of shoot growth in *Hevea brasiliensis*, the rubber tree, and the resulting morphological record are representative for most temperate and many tropical trees and, therefore, will be described in detail (Fig. 10.2) (4). The resting terminal bud, enclosed by bud scales, contains the inactive apical meristem with the primordia of nectaries (scalelike, reduced leaves bearing nectary glands) and the first foliage leaves (= preformed leaves). As the apical meristem enlarges,





**FIG. 10.2.** Periodic, indeterminate shoot growth in saplings of the tropical tree *Hevea brasiliensis* (rubber tree). (A,B) Rapid elongation of stem internodes between the nectaries and the first foliage leaves, and incipient expansion of new foliage leaves. (C) Sapling with four consecutive flushes of shoot growth and a stem cross section showing the corresponding periodicity in cambium growth (growth rings). (D) Periodic shoot elongation (—), shoot growth rate (· · ·), and continuous root elongation during three flushes of shoot growth lasting approximately 40 days each. (E,F) Spontaneous transition from periodic to continuous shoot growth (lampbrush) and the corresponding changes in length of petioles, leaf blades, and internodes. (G,H) Transition from periodic to continuous shoot growth resulting from experimental reduction in leaf area. (Redrawn from Ref. 4.)

the bud opens and the bud scales eventually abscise. Their closely spaced scars mark the limit between consecutive shoot increments (Fig. 10.2A,B). Nectaries, the first new foliar organs to appear on the elongating shoot, are separated by very long internodes indicative of rapid shoot extension (Fig. 10.2A,B). They are followed without transition forms by the first, largest foliage leaves of the flush (Fig. 10.2B). Subsequent leaves have progressively smaller blades and shorter petioles and internodes (Fig. 10.2B,C,E). An abrupt transition from the last foliage leaf to bud scales marks the end of shoot growth and formation of the new terminal bud.

The progressive reduction in internode length between the foliage leaves reflects a marked decline in the rate of shoot elongation. Young leaves thus

begin expanding during a period of declining shoot elongation, and petiole elongation and leaf blade expansion are completed well after the arrest of shoot growth. Periodic shoot growth is accompanied by periodic activity of the cambium, as indicated by the formation of growth rings in the wood (Fig. 10.2C), while simultaneous root growth is continuous (Fig. 10.2D).

The periodic shoot growth in *Hevea* thus involves not only an alternation between periods of rest and cell growth in the apical meristem but also a precisely timed, reversible transition between fully developed foliage leaves and reduced leaf organs such as bud scales and nectaries. The transition from foliage leaves to bud scales is developmentally similar to the transition from foliage leaves to bracts and flower organs, which precedes flowering. The reversibility of this developmental sequence is, however, unique to trees of the *Hevea*-type of development, which probably represents the most advanced and most adaptable of the many known patterns of tree growth (see also Chapter 1, this volume).

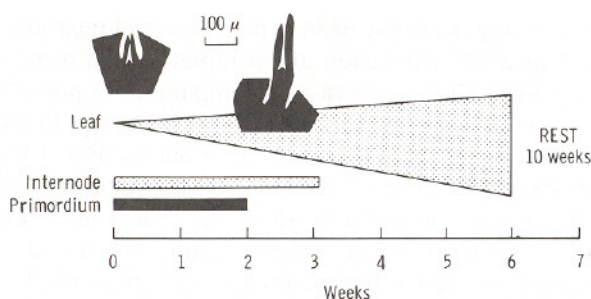
### 10.2.2. Variation in shoot morphogenesis

The temporal relations between rest, extension growth, and leaf morphogenesis are highly variable (1,7,11). During *determinate shoot growth* of temperate, broad-leaved trees, all leaves unfolding during the relatively short period of shoot growth arise from primordia preformed in the resting bud (Fig. 10.1a,b). Primordia for leaves expanding during the next growth episode, usually 1 year later, develop soon after the arrest of shoot growth within the resting bud. The prolonged, *indeterminate shoot growth* of trees such as *Populus* (poplar) or *Salix* (willow; Fig. 10.1d) also involves the expansion of leaves newly initiated at the apical meristem.

Different shoot growth patterns are observed among trees of the same species or even within the same individual tree. Saplings, stem sprouts, and vigorous leaders often exhibit relatively long periods of indeterminate shoot growth (Sections 10.3 and 10.4), whereas lateral shoots, such as short or spur shoots, have only a brief period of determinate growth. Similar variation in shoot morphogenesis exists among conifers (12,13); in *Pinus* and other genera foliar primordia may be preformed within the terminal bud as much as two seasons before they expand.

Many other tree species are unable to undergo reversion from foliage leaves to bud scales and hence do not form terminal buds enclosed by bud scales. In such trees, the shoot apex may be protected by the leaf bases or stipules of older leaves or may be naked, as in leguminous trees. Periods of shoot growth are terminated by irreversible morphogenetic changes in the apical meristem such as formation of a terminal inflorescence (e.g., *Aesculus* and many hapaxanthic tropical trees), abortion of the shoot tip [e.g., *Ulmus* (elm) and leguminous trees with naked buds], or parenchymatization of the apical meristem, as common in tropical trees. Subsequent shoot growth originates from lateral buds subtending the transformed or aborted shoot tip, often resulting in characteristic branching patterns (Ref. 10; See also Chapter 1 in this book).





**FIG. 10.3.** Development of the apical bud in *Gnetum africanum*. After a rest period of 10 weeks, the internode, the existing pair, and the next pair of leaf primordia begin to grow simultaneously, but growth of the internode and the new primordia is arrested, presumably by correlative inhibition, long before leaves are fully expanded. (Redrawn from Ref. 14.)

### 10.2.3. Continuous shoot growth

Evergreen trees of slow, continuous growth are confined to the wet tropics (1,2,10). Trees such as palms, *Rhizophora mangle* (mangrove), *Schefflera*, and *Gnetum africanum* (10,14) may produce a leaf or leaf pair every few months, and periods of extension growth and morphogenesis alternate with relatively long periods of rest (Fig. 10.3). Continuous shoot growth is thus characterized by the lack of morphogenetic changes at the shoot apex, but not necessarily by a constant rate of shoot extension.

## 10.3. Correlative growth inhibition in constant environments

### 10.3.1. The regulation of periodic shoot growth

The most puzzling aspect of periodic growth in trees is the cessation of shoot growth under environmental conditions that permit continued growth of herbaceous plants and seedlings of many tree species. Only when we understand the inhibitory factors involved will we be able to define the state of the inactive meristem and the conditions required for the resumption of growth. We must therefore address the following questions: Which physiological factors arrest extension growth, alter the morphogenetic pattern, and induce rest in the apical meristem? How do these factors arise in trees growing under favorable conditions? What causes the inhibitory factors to eventually disappear and permit the resumption of shoot growth in the absence of apparent environmental triggers? How is the duration of the rest period determined?

### 10.3.2. Experimental modification of shoot growth patterns

*A priori*, one would expect the maintenance of a functional equilibrium between growing shoots and other organs to be a prerequisite for continuous

growth. For instance, the remarkably constant dry-weight ratios between root and shoot found in many seedling populations (15,16) suggest the existence of mechanisms regulating the balance of growth between root and shoot. Indeed, most experimental treatments modifying shoot growth periodicity affect the root : shoot ratio or the functional equilibrium between a tree's root and shoot system.

A spontaneous transition from periodic to continuous shoot growth, resulting in the "lampbrush" growth form, is occasionally observed in young *Hevea* trees. Lampbrush trees have relatively small leaves and short internodes, indicative of a low rate of shoot extension (Fig. 10.2E,F) (4). Similarly, in the wet tropics, the main shoot (leader) of several species of *Pinus* may grow continuously and form unbranched "foxtails" more than 10 m in length (11). Transition from periodic to continuous growth can be induced experimentally in *Hevea* by reducing each expanding leaf to one-third its normal size (Fig. 10.2G,H). Successive removal of immature leaves results in continuous growth in saplings of other species (14,17,18).

Defoliation of temperate trees during the summer by experimental manipulation, severe drought, insect attack, or hailstorms, may cause renewed growth of arrested terminal and lateral buds in late summer (7), and occasional dry periods in tropical rain forests result in leaf shedding and subsequent flushing in evergreen trees (Refs. 2,19; Section 10.5.2). Potted saplings of *Hevea* and several temperate trees grow continuously for many months in the high humidity of the greenhouse environment (7).

The arrest of shoot growth by restriction of root growth is illustrated by the well-known slowdown and eventual cessation of growth in *pot-bound* plants. Shoot growth in potted saplings of *Quercus* is arrested whenever they reach a certain leaf area but resumes after transplanting into larger containers (6). The effect of an increased root : shoot ratio is dramatically illustrated by the rapid, continuous growth of stem sprouts or coppice shoots; e.g., sprouts of *Quercus* may grow continuously, rather than periodically, for several months (5).

### 10.3.3. Periodic root growth

In contrast to the continuous root growth of *Hevea* saplings (Fig. 10.2D), periods of root growth alternate in the majority of trees with periods of shoot growth. In temperate trees root growth begins in spring several weeks before bud break, slows down or stops during flushing, and resumes after the arrest of shoot growth (20). In tree seedlings, the temporal, and implicitly functional, relations between periodic root and shoot growth are precise: each period of rapid root growth is immediately followed by the resumption of shoot growth. Inversely, root growth appears to be inhibited by shoot growth, as indicated by its rapid decline during the initiation of shoot growth (Fig. 10.4) (16,18,20).

### 10.3.4. Arrest of shoot growth by water deficits

The establishment or maintenance of a relatively large root : shoot ratio by reduction of leaf area or increased root growth enables continued shoot growth

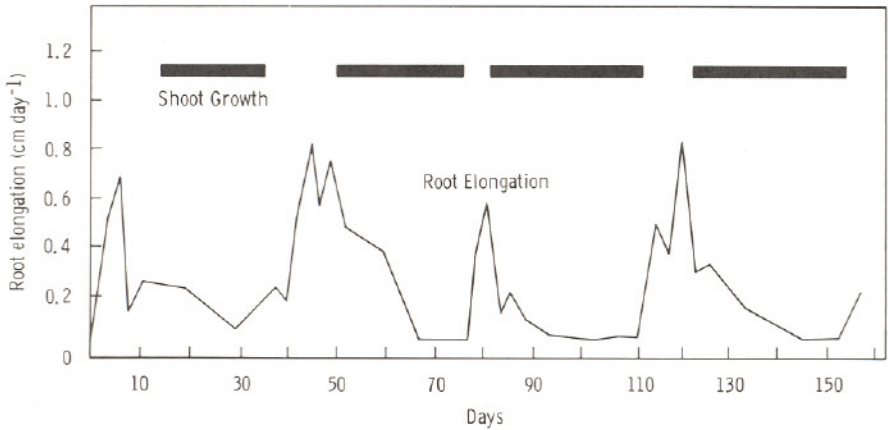


FIG. 10.4. Periodicity of shoot and root growth in 2-year-old seedlings of *Quercus alba*. (Redrawn from Ref. 20.)

or the resumption of growth in resting buds of small trees (Section 10.3.2). Implicitly, these events relieve the restriction of shoot growth imposed earlier by a functional imbalance between root and shoot. This type of inhibition of one organ by another is defined as *correlative inhibition* (1,7). The resulting bud rest will be referred to as *correlative rest*.

When pot-bound tree seedlings are transplanted to larger containers, shoot growth resumes without defoliation (6). Leaves thus inhibit shoot growth only if deficient in a factor provided by the root system in proportion to its size. The most important substance supplied by the roots and continuously required by leaves in substantial amounts is water. *Internal water deficits resulting from an unbalanced root : shoot ratio thus constitute the most likely physiological basis for the correlative inhibition of shoot growth by leaves and the cause for*

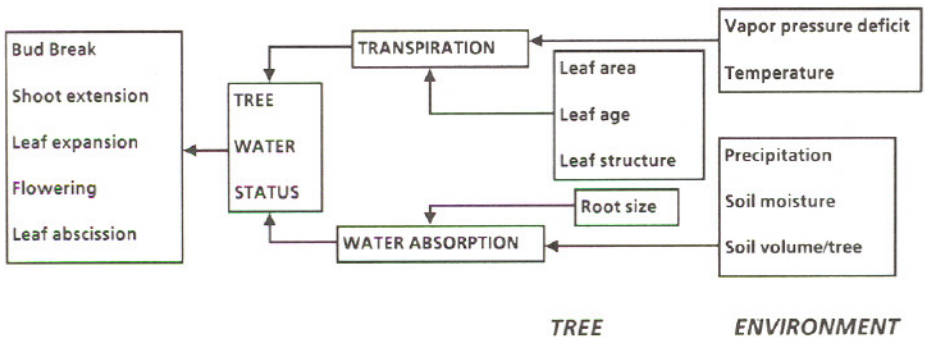


FIG. 10.5. Biotic, environmental, and climatic factors affecting the water status and development of trees.



**Table 10.1.** Effects of root restriction on growth correlations and water relations of alder seedlings<sup>a</sup>

Variable	Treatments			
	500	16	6	1
Root volume (ml)	1050	800	400	160
Leaf area/plant (cm <sup>2</sup> )	13	17	5	1
Transpiration/plant (mg s <sup>-1</sup> )	-0.7	-1.1	-1.35	-1.8
Water potential, 5th leaf (mPa)	10		10	25
Noon diffusive resistance (s cm <sup>-1</sup> )	0.25		0.1	0.13
Root : shoot ratio (dry weights)				

<sup>a</sup>The roots of seedlings of *Alnus glutinosa* (48 days old, 4.5 cm height) were placed into perforated polypropylene test tubes (1.5, 6, 16 ml), which prevented roots from growing out, and were set into a 500-ml container containing aerated nutrient solution. Roots of "unrestricted" control seedlings grew directly in the 500-ml container. Measurements were taken after 70 days of treatment. (Data adapted from Ref. 21.)

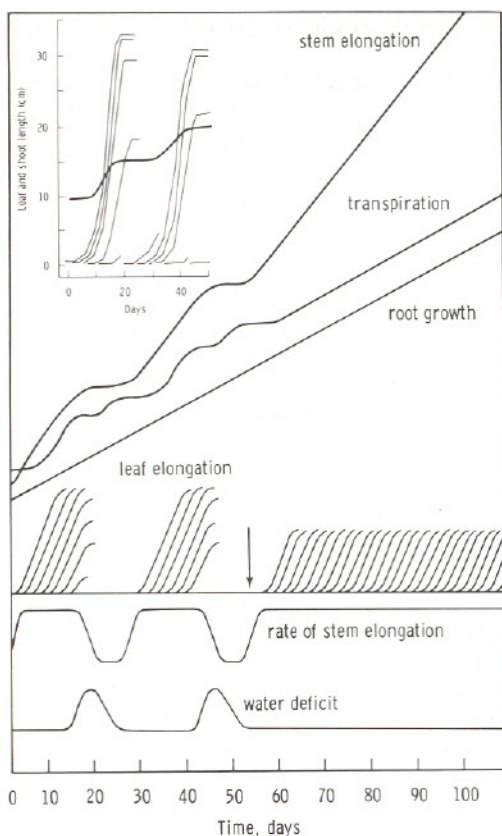
the arrest of shoot growth during periodic growth. Defoliation or cultivation of tree seedlings in high humidity (Section 10.3.2) would thus permit continuous shoot growth by preventing the development of water deficits causing arrest of shoot growth (Fig. 10.5).

In seedlings of *Alnus* (alder) growing in nutrient solution, progressive restriction of root volume results in a lowered root : shoot ratio, decreasing leaf water potentials, and arrest of shoot growth (Table 10.1) (21). Inversely, removing one-third of the stem and its leaves from the top of *Populus* seedlings reduces water stress in the remaining shoot and releases lateral buds from correlative inhibition (22). The reduced growth of lateral tree branches as compared to that of the leader has been attributed to a reduced water supply of the laterals (23). There is thus good experimental evidence for the role of water deficits in various types of correlative inhibition in trees.

Correlative inhibition by the root is unlikely to be the result of deficiencies in root-produced plant hormones such as cytokinins. However, abscisic acid formed in water-stressed leaves might mediate the inhibitory effect of internal water deficits (Section 10.7).

#### 10.3.5. Computer simulation

The dynamic interaction among several variables, as involved in any type of correlative inhibition, cannot be verified by experiments such as those described, which necessarily involve destructive sampling. Correlative inhibition of shoot growth by the root system was therefore computer-simulated (Fig. 10.6) (24). Simulation yields patterns of periodic shoot growth remarkably similar to those observed in young trees of *Theobroma* grown under constant conditions. Shoot and leaf growth are arrested simultaneously in *Theobroma*, presumably by an internal water deficit. Reducing leaf size in the simulation decreases transpiration and results in continuous shoot growth, as achieved experimentally in *Hevea* (Fig. 10.2G,H).



**FIG. 10.6.** Computer simulation of rhythmic shoot growth. During the beginning of each flush the stem elongates and leaves expand in rapid sequence, causing a rapid increase in leaf area and transpiration. When water loss by transpiration exceeds water absorption by the continuously growing root, a water deficit develops and causes termination of stem and leaf growth. Shoot growth resumes when the water balance has been restored by root growth. Reduction of leaf length by 45% after day 50 reduces the rate of increase in leaf area and transpiration to the rate of root growth, achieving a balanced water economy and continuous growth of the tree (compare Fig. 10.2G). Inset: Periodic shoot elongation (thick line) and leaf growth (thin lines) in saplings of *Theobroma cacao* under constant environmental conditions. (Redrawn from Refs. 3,24.)

The computer model illustrates how periodic growth under constant environmental conditions can result from interaction between *any* two, potentially continuous partial processes, if the slower process is rate-limiting for the faster one. The repeated alternation between feedback inhibition and growth will manifest itself as an endogenous growth rhythm of constant period length (Figs. 10.2D, 10.3, 10.6). Feedback inhibition by internal water deficits represents only one of several conceivable mechanisms. However, the model



(*Hevea*, *Theobroma*; Figs. 10.2, 10.6) to 4 in mature *Theobroma* and *Camellia thea* (tea), and to 1 or 2 in most other trees.

Similar age-related changes in growth-periodicity occur in temperate trees. In *Quercus* the number of seasonal flushes declines from 3–4 in seedlings to 1–2 in mature trees. In *Acer*, *Fraxinus* (ash), and *Prunus* seedlings grow continuously, but *saplings* may undergo temporary reductions in growth rate accompanied by partial transformation of leaves into bud scales, then resume rapid growth, and finally form a resting bud in fall. In mature trees shoot growth usually ceases by midsummer (Fig. 10.1) but may resume after defoliation by insect damage or drought (Section 10.3.2).

## 10.5. Seasonal drought

### 10.5.1. Tree development and seasonal drought

In many tropical regions, seasonal variations in temperature and photoperiod are small, but fluctuations in rainfall are great. In Costa Rica, at a latitude of 10°N, the variation of monthly temperatures from the annual mean is about 1°C and the photoperiod varies less than 30 min annually, but more than 95% of the annual precipitation falls between late April and early November (Fig. 10.7) (27). Considering climate, the major determinant of periodic growth, one would predict synchronized flushing of trees with the advent of rains in May, and no shoot growth during the 5 months of drought.

The annual course of development and water status in *Cochlosperum* and *Spondias* (Fig. 10.7) is representative of most trees in tropical deciduous forests (27). Changes in stem circumference (girth) are correlated with tree water potential and therefore indicate changes in tree water status (28). As expected, rapid rehydration of leafless trees after the first rains causes bud break, and the cessation of rainfall results in a rapid decline in soil moisture and tree water potential accompanied by leaf fall.

The phenological records in Fig. 10.8 describe the growth periodicity of several populations within two tropical tree species, *Erythrina poeppigiana* and *Tabebuia rosea*, growing along an altitudinal gradient on the Pacific slope of Costa Rica ranging from 40 to 1340 m (29,30). These populations differ in tree size, water availability, and evapotranspiration during the dry season. There is thus wide variation with respect to the biotic and environmental factors affecting tree water status (Fig. 10.5).

Even a glance at the phenological records reveals that seasonal patterns of shoot development among the different tree populations of these species are far from synchronous and poorly correlated with seasonal climatic changes. Such a lack of predicted correlations between climate and tree development was noted in many studies of tropical tree phenology and led to speculations considering slight fluctuations in temperature and photoperiod as causes for growth periodicity (2,27). However, a critical reanalysis shows that the observed growth patterns correlate well with temporal changes in tree water status, supporting the role of water deficits in correlative rest (Section 10.3.4).



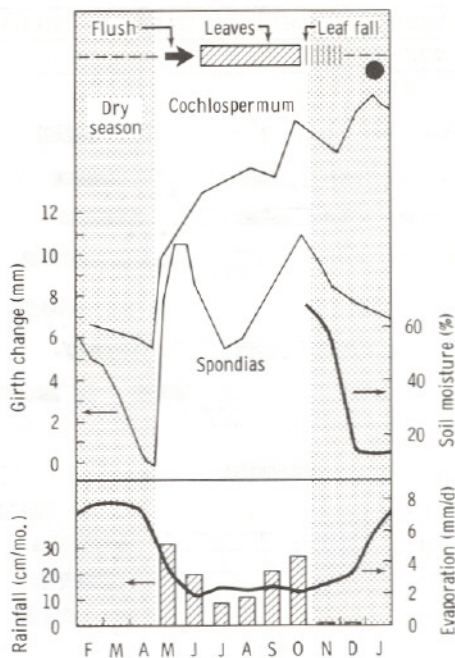


FIG. 10.7. Seasonal development and water status of *Cochlospermum vitifolium* and *Spondias purpurea* as a function of climate in the tropical deciduous lowland forest of Costa Rica. Relative change in girth of stem reflects changes in tree water potential. Seasonal changes in climate are indicated by changes in rainfall (bars), evaporation (lower curve) and soil moisture (curve: center right). The black dot indicates flowering in *Cochlospermum*. (Redrawn from Ref. 27.)

### 10.5.2. Leaf fall and bud break

Whenever *Erythrina* or *Tabebuia* shed their leaves during the wet season, new shoot growth starts before or immediately after leaf fall is complete (Figs. 10.8A–C,E,H,I; 10.9). This habit of *leaf exchange* has been described for many evergreen tropical trees (2). Watering of potted *Theobroma* saplings after a period of imposed drought causes renewed flushing only if preceded by partial shedding of leaves (19,26). The *induction of bud break by defoliation*, considered exceptional in temperate trees (Section 10.3.4), thus represents the normal developmental sequence in tropical trees.

Defoliation enables shoot growth by eliminating internal water deficits (Section 10.2.4). During the dry season, water stress in two large *Erythrin*as increased with leaf expansion and caused the abscission of young leaves. When water stress was relieved with the onset of the rains, new shoots emerged before leaf fall was complete (Fig. 10.9) (29). Resumption of growth in resting vegetative buds thus constitutes a reliable biological indicator for the elimination of water stress after leaf shedding. Inversely, a delay in the resumption of shoot growth after leaf fall indicates that drought has prevented full relief

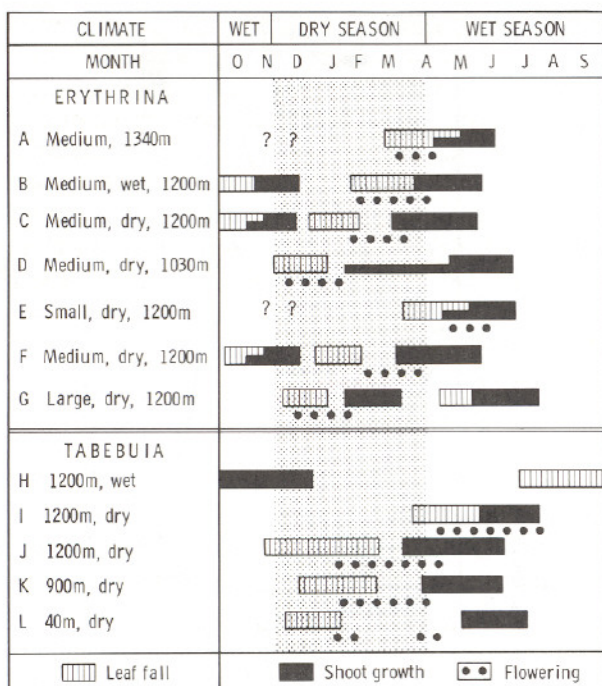
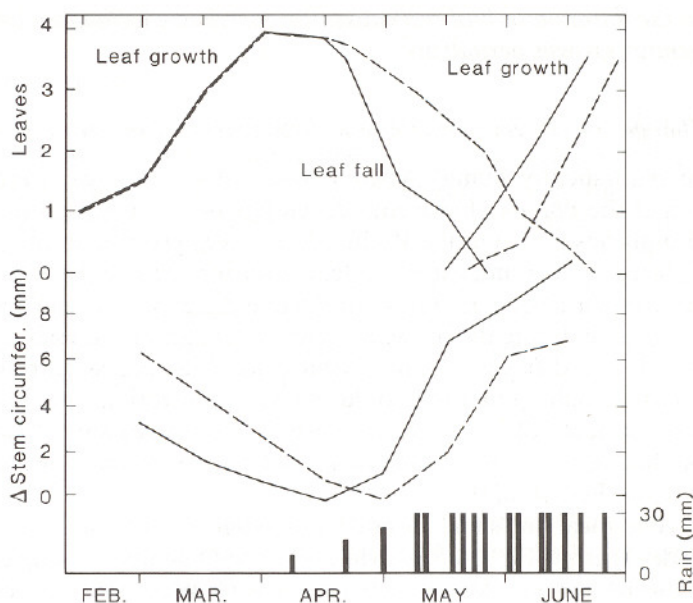


FIG. 10.8. Periods of seasonal development in *Erythrina poeppigiana* and *Tabebuia rosea* along an altitudinal gradient on the Pacific slope of Costa Rica ranging from 40 to 1340 m. Wet sites were within 10 m of a river; dry sites were at least 15 m away from a river. Tree size ranged from 2 to 3 m (small) to >20 m (large). After shoot growth and leaf expansion, trees were in full foliage until leaf fall occurred. (Redrawn from Refs. 30,32.)

from water stress (Fig. 10.7) or that fully hydrated buds are dormant (Section 10.6.1).

Like leaf expansion, the opening of flower buds (anthesis) involves cell expansion and is therefore sensitive to water stress. In *Erythrina*, *Tabebuia*, and many other tropical trees, flowers open during or immediately after leaf fall. Opening of flower buds is thus correlatively inhibited by senescent foliage and triggered by the elimination of water stress after leaf shedding (31). In *Cochlospermum*, drought-induced leaf shedding results in a reduction of water stress followed by anthesis (Fig. 10.7). Flowering, in turn, enhances water stress, as is also observed during flowering in leafless *Tabebuia* (28). The delayed bud break in trees flowering during the dry season (Fig. 10.8C,D,J,K) is probably due to water stress resulting from the unfolding of the large and relatively long-lived flowers of *Erythrina* and *Tabebuia* (30,32); flowers would thus inhibit bud break correlatively.

In conclusion, the developmental sequence *leaf fall* → *flowering* → *flushing*, observed in evergreen and deciduous tropical trees, represents a *bona fide* causal sequence regulated in time by the successive correlative changes af-



**FIG. 10.9.** Relations between leaf growth and tree water status (indicated by changes in stem diameter) in *Erythrina* (compare Fig. 10.7G). Stages in leaf development range from small, light green leaves (1) to mature, dark green foliage (4), and from 10% leaf fall (3.5) to complete leaf shedding (0). (Redrawn from Ref. 29.)

fecting tree water status. The central role of leaf fall in breaking correlative bud rest is obscured in temperate trees by the temporal separation of leaf fall and bud break by the cold season, and thus has not been adequately recognized in the past. This raises the question concerning the control of leaf fall as the first step in this sequence.

### 10.5.3. Leaf longevity

Leaves have a finite, species-specific life expectancy, which in tropical trees ranges from less than 6 months for delicate leaves to more than 2 years for coriaceous leaves (2,33). Toward the end of their life span, leaves become inefficient in photosynthesis and stomatal control; e.g., weeks before they are shed, older leaves in *Tabebuia* (Fig. 10.8H) and other species lose stomatal control, resulting in considerable water stress (34). In tropical rainforests, occasional dry spells cause massive abscission of such senescent leaves and subsequent flushing on individual branches of evergreen trees (Section 10.5.2).

Irrespective of site, *Erythrina* sheds leaves and then flushes twice a year as compared to only one annual growth cycle in *Tabebuia*. Lack of environmental triggering of leaf fall is apparent in *Erythrina* during the wet season (Fig. 10.8B,C,G) and in *Tabebuia* at dry and riparian sites (Fig. 10.8H-J). *In the absence of seasonal environmental stress, the longevity of leaves thus*



determines the duration of bud rest caused by correlative inhibition, and hence the endogenous growth periodicity.

#### 10.5.4. Changes in growth periodicity with increasing drought

Along the permanently humid Atlantic slope of Costa Rica, *Erythrina* is evergreen and the phases of seasonal development occur asynchronously in individual branches (29). On the Pacific slope, trees growing in the premontane moist forest flower and exchange leaves during the late dry season; i.e., they are evergreen (Fig. 10.8A). With decreasing elevation and increasing evapotranspiration during the dry season, leaf fall begins progressively earlier (Fig. 10.8A–D), and flowering and flushing occur in succession rather than simultaneously, resulting in a period during which flowering trees stand leafless. At 1030 m, leaf fall and flowering early in the dry season is followed by bud break, but new leaves remain small and fail to expand fully until the advent of rains (Fig. 10.8D).

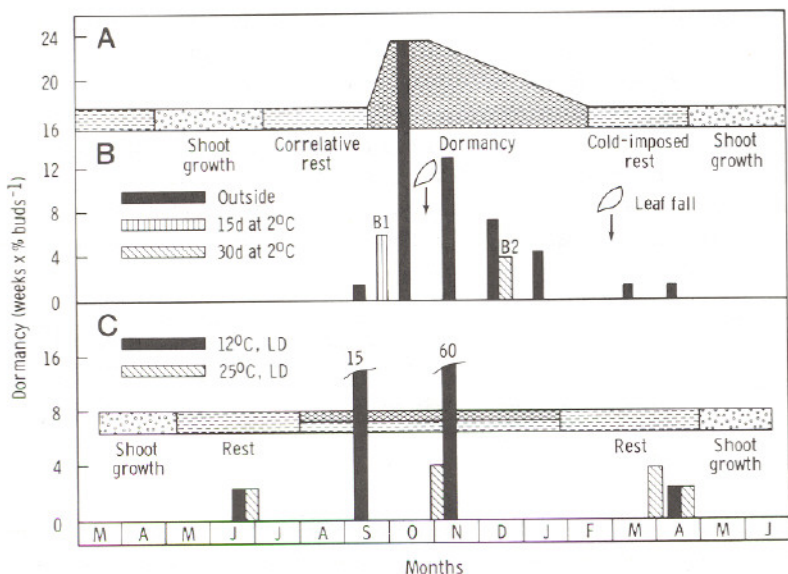
At the same location, small, pruned *Erythrina* change leaves and flower late in the dry season (Fig. 10.8E), while leaf shedding and subsequent flowering and flushing occur progressively earlier with increasing tree size (Figs. 10.8F,G; 10.9). This pattern parallels the trend along the altitudinal gradient of increasing drought (Fig. 10.8A–D) and confirms the effect of tree size on growth periodicity (Section 10.4).

Within the same species, increasing seasonal drought thus causes characteristic changes in growth periodicity. In an aseasonal climate, development is asynchronous within the crown of evergreen trees, slight seasonal drought synchronizes leaf exchange and flowering (Fig. 10.8a,b), and moderate drought imposes a deciduous habit with temporal separation of successive developmental phases (Fig. 10.8C,D). Throughout the range of *Erythrina*, leaf fall is the primary developmental and correlative change triggering anthesis and bud break by reducing water stress.

Increasing drought affects growth periodicity in opposite ways: on one hand, it accelerates leaf shedding and thus rehydration, flowering, and flushing; on the other hand, drought depletes soil water and prevents buildup of the high water potential required for shoot growth. These trends are apparent over the range of *Tabebuia* (Fig. 10.8I–L). At higher elevations anthesis occurs after leaf fall, but flushing is delayed by seasonal drought (Fig. 10.8I–K). At 40 m, release from water stress by leaf shedding permits only partial anthesis. The remaining flower buds open after the first rains just before the resumption of shoot growth (Fig. 10.8L; compare *Cochlospermum* in Fig. 10.7). In *Tabebuia neochrysantha* and other species isolated, heavy rain during the dry season causes rapid rehydration of trees and mass flowering in tropical deciduous forests (28). With increasing seasonal drought the interval between leaf shedding and bud break becomes progressively longer (Figs. 10.8K,L; 10.7). Leaf shedding is insufficient to relieve water stress, and drought prevents rehydration and bud break in leafless trees, which thus remain in a state of drought-imposed rest.

growth potential associated with dormancy must be assessed experimentally. *Bud dormancy* is evaluated by transferring entire, defoliated tree seedlings, stem cuttings, or isolated internodes bearing a single bud to optimum growing conditions (Fig. 10.11). Under such conditions *resting buds* will resume growth within 10 days (Fig. 10.11B, Sep., March). With increasing intensity of dormancy, the time to bud break increases to several weeks or months (Fig. 10.11B, Oct.–Jan.).

The growth pattern in potted seedlings of *Fraxinus* growing in Europe illustrates the course of seasonal development in most temperate, broad-leaved trees (Fig. 10.11A,B). After a flush of shoot growth in spring, by midsummer terminal buds of the seedlings enter a state of *correlative rest*, which can be broken by defoliation as late as September. Thereafter, short photoperiods and declining temperatures of autumn cause a rapid transition from *rest* to intensive *dormancy* (Fig. 10.11B, Sep.–Oct.). The intensity of dormancy declines from October to January, and by February dormant buds have returned to a state of rest. This time course suggests that the main adaptive value of dormancy is to prevent bud break in fall, which would result in the death of the new shoots during winter (compare Fig. 10.10B). During February and March, resumption of shoot growth under field conditions is



**FIG. 10.11.** Seasonal development and bud dormancy in seedlings of *Fraxinus excelsior* (ash). (A) Annual course of shoot growth, bud rest, and dormancy in potted seedlings exposed to climatic conditions of central France. (B) Changes in the growth potential of terminal buds of defoliated seedlings transferred from the outside to a growth chamber (25°C, 16 h light). Dormancy units were calculated by dividing weeks to budbreak by the fraction of plants on which budbreak occurred. (B1, B2) Seedlings transferred to growth chamber after receiving the indicated treatment. (C) Seedlings maintained at 12 or 25°C and 16-h photoperiod (LD). (Redrawn from Refs. 36–38.)



delayed by low temperature (Fig. 10.11A,B), and buds are thus in a state of *cold-imposed rest*, analogous to the *drought-imposed rest* of tropical trees during drought (Section 10.5.4).

### 10.6.3. *The effect of chilling*

A low-temperature treatment of *Fraxinus* seedlings early in the winter enhances the *induction of dormancy*, but cold exposure at a later time causes the *breaking of dormancy* [Fig. 10.11, B1, B2]. The effect of chilling thus varies with the physiological state of the dormant bud. Under natural conditions, breaking of dormancy in temperate trees requires an exposure to low temperatures for a minimum period. This *chilling requirement*, the intensity of dormancy, and cold-hardiness are correlated within species, ecotypes, and cultivars of woody plants, reflecting the adaptive nature of these characters. Temperate fruit trees range from a high chilling requirement, good cold-hardiness, and late bud break in varieties suited for the northern temperate zone to varieties with low chilling requirements for warm temperate and subtropical climates (39).

### 10.6.4. *Role of photoperiod*

If dormancy and cold-hardiness are to protect temperate trees against freezing damage, physiological changes must occur before trees are actually exposed to the first frost. *A priori*, the progressively shorter photoperiods of autumn, rather than declining temperature, should thus be the principal environmental signal inducing dormancy and cold-hardiness in anticipation of the coming of winter (7,17). This is in marked contrast to drought adaptation, where water stress itself causes the adaptive developmental changes such as enhanced leaf shedding and arrest of shoot growth (Section 10.5).

In mature temperate trees, shoot growth is arrested long before fall (Fig. 10.1) and bud rest is therefore *not* caused by exposure to short photoperiods. Because of the difficulty of working with such trees, the relative contribution of photoperiod versus low temperature to the induction of dormancy is not known. Saplings of both tropical and temperate trees respond to short photoperiods (8–10 h) with a reduction in shoot extension, which may or may not be followed by the formation of resting buds (7,17). In many species, growth is immediately resumed when plants are returned to long photoperiods, but some temperate species become dormant and require chilling before growth can be resumed. Similarly, exposure to long photoperiods prevents the induction of dormancy in many, but not all, temperate species (e.g., Fig. 10.11C). In *Corylus* seedlings short photoperiods without simultaneous cold exposure cause an arrest of shoot growth and dormancy, but do not trigger the morphogenetic changes normally associated with dormancy induction (Fig. 10.10A,C).

Photoperiod thus plays an important role in the control of seasonal development in temperate trees, but responses to photoperiod vary widely among



species and do not permit a distinction as to whether photoperiod induces bud rest, dormancy, or cold-hardiness. Photoperiodism, like hormonal control (Section 10.7), is thus only one among several regulatory mechanisms.

#### 10.6.5. Induction of dormancy under constant conditions

Dormancy has been observed in equatorial forests around the world (Section 10.6.1). In equatorial Kenya and Java, bud dormancy in apple trees (*Malus*) can be prevented by defoliation soon after harvesting the fruit (39,40). Dormancy develops and then disappears when *Fraxinus* seedlings are grown under long days at 12°C, but not at 25°C (Fig. 10.11C). Trees can thus become dormant without exposure to variations in photoperiod or temperature, and the biochemical changes associated with the transition of buds from rest to dormancy are primarily endogenous in nature, but can be affected by the environment.

### 10.7. Hormonal regulation

The hypothesis that bud dormancy in trees might be caused by inhibitory plant hormones, such as abscisic acid (ABA), was introduced 40 years ago, since the level of growth inhibitors in extracts from dormant *Fraxinus* buds declined during winter in parallel with bud dormancy. Later, it was proposed that short photoperiods cause an increase in the ABA content of buds, while chilling reduces ABA levels and thus enables bud break in spring. None of these hypotheses withstood experimental testing (41,42), and the following assessment of hormonal control of bud dormancy, written 25 years ago, remains valid (7): "Our knowledge of endogenous growth regulators (including morphogenetic receptor pigments), and their interactions under various conditions, is so inadequate that intelligent discussion of the subject is not yet possible." Indeed, neither shoot growth periodicity nor any other aspect of plant development involving correlations between organs (e.g., apical dominance, flower induction, or tuber formation) has been satisfactorily explained in terms of hormone interactions (43). The genetic and physiological control of morphogenesis is so complex even in a relatively simple system such as the isolated shoot meristem of tobacco (44) that any attempt to deduce hormonal control of shoot growth periodicity in woody plants from crude correlations between extracted hormones and shoot development appears overly simplistic. There can be little doubt that plant hormones are involved in the regulation of growth periodicity. However, the complex interrelations between environmental (photoperiod, drought, and cold), nutritional, and hormonal factors remain to be unraveled.

Much of the evidence for the involvement of plant hormones in the regulation of dormancy is of limited value, because the physiological state of the analyzed buds has seldom been defined. Observed hormonal changes claimed to be correlated with the onset and breaking of bud dormancy are more likely

to be associated with bud rest. During periodic shoot growth in *Citrus* and *Quercus* seedlings the ABA level is lowest just before flushing (5), and bud break caused by defoliation in *Theobroma* and *Malus* grown in the tropics is preceded by a decline in ABA content (45). In many temperate trees, endogenous levels of ABA are lowest immediately before bud break in spring, i.e., months after the chilling requirement has been met and dormancy has ended (41). In *Prunus cerasus* (sour cherry), defoliation in autumn prevents an increase in ABA, but not bud dormancy. Levels of growth-promoting hormones such as auxin, gibberellins, and cytokinins generally increase before bud break, suggesting that the ratio between ABA and growth-promoting hormones might control the induction and breaking of dormancy or rest.

The arrest of shoot growth and formation of terminal buds by an ABA treatment of seedlings of *Betula* and other species under long-day conditions (41) represents an induction of rest rather than dormancy, because growth resumes soon after the treatment ends. Inversely, treatments with gibberellins can stimulate the growth of resting buds that have partly emerged from dormancy, but do not break dormancy. For every example describing a specific effect of externally applied hormones, there are others in which applied hormones were ineffective in inducing or breaking bud rest, or in which no correlation between hormone content and activity of the apical meristem was found. None of the proposed hypotheses has thus been conclusively confirmed.

Water deficits, the major factor involved in the induction of correlative rest (Sections 10.3.4 and 10.3.6) cause elevated levels of ABA in leaves. This growth inhibitor is then transported to sinks such as growing apical meristems (46). The implicit correlation between the disappearance of water deficits and decreased ABA concentration prior to bud break induced by defoliation raises the unexplored question of whether internal water deficits affect apical meristems directly or indirectly via the induction of ABA synthesis.

In many instances, the chilling requirement for the breaking of bud dormancy in woody plants as well as tubers and corms can be eliminated by bud scale removal, soaking in warm water, anaerobiosis, or treatments with various chemicals, including metabolic poisons. Changes in respiration and nucleotide metabolism associated with the breaking of bud dormancy indicate a reduced energy metabolism during dormancy (8,38), but such changes might be the consequence rather than the cause of dormancy.

## 10.8. Periodic growth and the adaptive strategy of trees

Periodic shoot growth of trees, characterized by the temporary arrest of growth under favorable growing conditions (correlative bud rest), results primarily from the interaction among the organs of a tree. As a tree increases in size and hence in the number of interacting organs, the pattern of shoot growth periodicity changes as a consequence of changing functional correlations. Water deficits resulting from an excess of transpiration over water



absorption appear to be the principal cause of shoot growth cessation. Elimination of water deficits, and thus correlative inhibition, by shedding of leaves causes the termination of correlative bud rest and the resumption of shoot growth. In nonseasonal climates, the interval between consecutive episodes of leaf fall and shoot growth, i.e., the period length of shoot growth rhythmicity, is therefore a function of the species-specific longevity of a tree's leaves, and shoot growth periodicity is ultimately the consequence of the periodic, simultaneous replacement of a tree's foliage. Only trees that form and replace leaves slowly and gradually are able to sustain continuous, but slow, growth.

Adverse environmental conditions such as drought or cold may prevent the resumption of shoot growth even after leaf fall. Consequently, trees are leafless during periods of drought- or cold-imposed bud rest, and shoot growth resumes as soon as environmental stress is relieved. The endogenous shoot growth rhythmicity may thus be adapted secondarily to seasonal changes in climate. Finally, resting buds may become dormant, i.e., temporarily lose the potential to resume growth when exposed to favorable growing conditions. Periodic growth patterns *per se* are therefore not genetically determined, but result from the interaction among a variety of endogenous and environmental factors.

Earlier attempts to explain the adaptive significance of growth periodicity and rest periods have considered these phenomena in isolation rather than viewing trees as large, long-lived plants with a characteristic strategy for maximizing carbon gain (47,48). At the beginning of each episode of shoot growth, reserve assimilates are invested in the growth of branches and leaves, resulting in the rapid establishment of a full complement of leaves. Carbon gain from the mature foliage is then used for growth in girth, to replenish assimilate reserves for the next phase of shoot growth and, eventually, to produce seeds. In trees with a full crown of productive leaves, shoot growth is arrested to reduce self-shading and should resume soon after leaf fall. In view of the trade-off between carbon gain and water loss, the central role of water stress in the proximate mechanisms regulating tree growth periodicity is to be expected.

Periods of imposed rest and dormancy in leafless trees reflect delays imposed on the normal reestablishment of photosynthetic surfaces by environmental stress such as drought or cold; environmentally imposed bud rest thus represents tolerance of, rather than adaptation to, environmental stress. In contrast, bud dormancy and cold-hardiness are truly adaptive, because these temporarily acquired physiological states enable temperate trees to survive cold winters.

#### ACKNOWLEDGMENTS

The author gratefully acknowledges critical review of the manuscript by Dr. C. Martin and careful execution of the illustrations by S. Hagen.

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