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Phenology and Control of Flowering in Tropical Trees

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ABSTRACT

Descriptions of structure and flowering phenology of the tropical tree species *Cedrela mexicana*, *Cordia glabra*, *Erythrina poeppigiana*, *Tabebuia rosea*, and *Tabebuia ochrea* ssp. *neobrysantha* are used to analyze and illustrate the complex relations between structure, vegetative development, and flowering in tropical trees. Because of the strong positional differentiation within tree crowns and the repetition of vegetative and reproductive growth cycles in trees, flower development and its control are more complex than in herbaceous plants. Formation of terminal inflorescences, as found in *Cedrela*, *Cordia*, and *Tabebuia*, regularly occurs at the end of a flush of determinate shoot growth; flower initiation, like shoot growth cessation, is therefore controlled by internal, correlative factors rather than by environmental changes. Initiation of lateral inflorescences is usually preceded by growth cessation in the indeterminate, vegetative shoot, but the timing and control of flower induction in lateral buds are unknown. For many tropical trees, particularly those growing in seasonal climates, flower development is discontinuous, i.e., flower initiation and anthesis are separated by a prolonged rest period and must be controlled separately. Delayed anthesis is usually triggered by rehydration of previously water-stressed trees resulting from leaf shedding or, in dry habitats, by rainfall. Because of different degrees of seasonal water stress, leaf fall and subsequent anthesis in several species extend over three to four months. The observed periodicity of anthesis in tropical trees is thus largely determined by seasonal changes in tree water status and is unlikely to be the result of selection for optimum tree-pollinator interaction.

IN MOST TROPICAL TREES, flowering, like vegetative growth is episodic, and seasonal peaks of flowering have been recorded for many tropical forests (e.g., Fournier and Salas 1966, Janzen 1967). During recent years, tropical ecologists have considered the temporal pattern of flowering the result of coevolution of trees with pollinators and seed predators. It has been argued that peaks of flowering occur during periods of high pollinator activity, and that overlapping, but different, flowering periods in related species reduce competition for pollinators and assure a continuous source of nectar to pollinators (Janzen 1967, Gentry 1976, Stiles 1978). If the temporal pattern of flowering is adaptive, then mechanisms for the specific timing of flowering must have evolved in tropical trees. The timing of flowering in tropical trees usually has been ascribed to environmental control mechanisms analogous to those that have evolved in temperate plants to adapt vegetative and reproductive development to a growing season of limited duration (Larcher 1980). Relations between tree architecture, vegetative growth and flowering of tropical trees have been rarely considered.

In this paper, I shall use descriptions of the flowering behavior of five tropical tree species as a basis for discussing the relations between tree architecture, vegetative development, and flowering, as well as our scant knowledge of their internal and environmental controls. I will show that evolution of the temporal pattern of flowering in tropical trees cannot be adequately explained as resulting from biotic interactions alone, but must be seen in the context of overall tree development as determined by a given set of climatic, edaphic, and biotic factors.

STUDY SITES AND METHODS

Most of the phenological observations on flowering of tropical trees discussed in this paper were made on the Pacific slope of Costa Rica, Central America, along an altitudinal gradient extending from the deciduous lowland forest of Guanacaste Province (Janzen 1967, Daubenmire 1972, Frankie *et al.* 1974, Opler *et al.* 1976, Reich and Borchert 1982, 1984) through the lower montane forest at Villa Colón (800 m altitude) and Santa Ana (900 m; Fournier and Salas 1966, Fournier 1969) to the Central Valley of Costa Rica (La Sabana, 1100 m; San Pedro Montes de Oca, 1200 m; Granadilla, 1350 m) (Fournier 1969, Borchert 1980). The climate in the entire area is characterized by a dry season lasting from late November to April/May and a wet season providing adequate rainfall (approx. 2000 mm) for the remainder of the year. With increasing altitude, the severity of the dry season diminishes and some species change from a deciduous to an evergreen habit (e.g., *Erythrina poeppigiana*, *Tabebuia rosea*; Fournier 1969, Borchert 1980).

The discussion of tree morphology is based on the analysis of tropical tree architecture by Hallé *et al.* 1978, where definitions of all morphological terms can be found.

MORPHOLOGY AND PHENOLOGY OF FLOWERING IN FIVE TROPICAL TREE SPECIES

TABEBUIA ROSEA (BERTOL.) DC, BIGNONIACEAE.—The shoot system of *T. rosea* is composed of many orthotropic, sym-

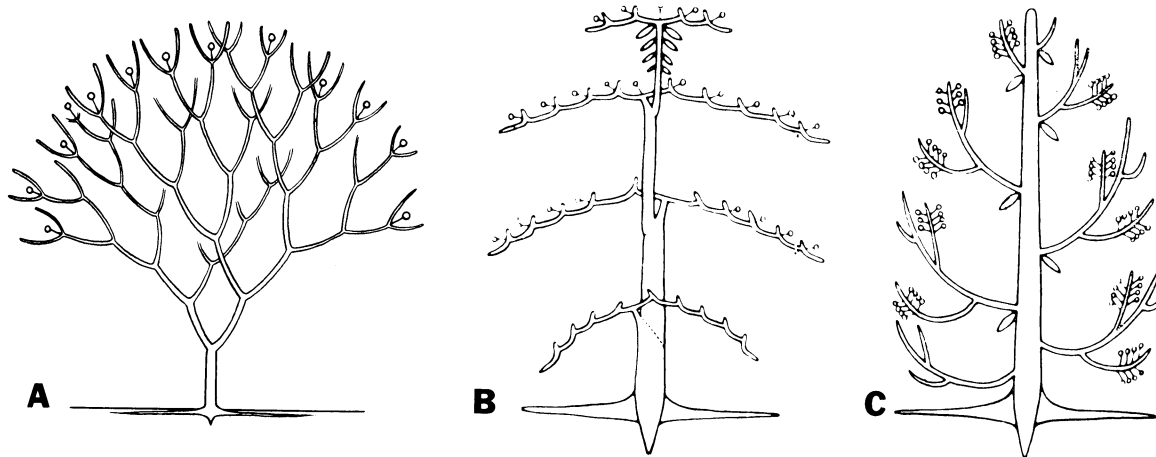


FIGURE 1. Architectural models of tropical trees (Hallé and Oldeman 1970). A. Branch system of *Tabebuia* composed of symphydially branched, equivalent, orthotropic shoots of determinate growth (modules) bearing terminal inflorescences (hapaxanthly; model of Leeuwenberg); B. Branch system of *Cordia* showing terminal flowers on plagiotropic lateral branch modules (hapaxanthly; model of Prévost); C. Branch system of *Erythrina*, lateral inflorescences are borne on indeterminate, orthotropic shoots (pleoanthly; model of Attims).

podially branched, equivalent shoot segments ("modules") of determinate growth, which usually, but not always, terminate in an inflorescence (Fig. 1A; *architectural model of Leeuwenberg*, Hallé *et al.* 1978; Borchert and Slade 1981). After the terminal meristem has differentiated into a flower bud, vegetative growth is continued by the symmetrical outgrowth of two subtending, opposite lateral buds (Fig. 2; *substitution growth*, Hallé *et al.* 1978).

The principal flush of shoot growth in *T. rosea* usually takes place during the early rainy season and is completed within two to three months. At mesic sites, many branches undergo a second flush. The small terminal flower buds of new shoots remain dormant for several months (Fig. 2). When leaves begin to abscise during the dry season, flower buds swell and the large, pink flowers open (Figs. 3A–D). Frequently, leaves in the upper part of the tree crown fall earlier than those in the lower part, and flowers open first on the bare, upper branches. Fruits develop during the months following anthesis, often simultaneously with the emergence of new shoots.

The timing of this sequence of seasonal development is highly variable. In the tropical lowland deciduous forest of Guanacaste, leaf shedding followed by flowering occurs during the early dry season (Frankie *et al.* 1974). Trees stand leafless for several weeks and flush after the first rains. At higher elevations with decreasing evaporative demand during the dry season, leaf fall and subsequent flowering occur increasingly later: at 800 m the peak of flowering was in February, at 940 m in late March, and at 1200 m in May/June (Fournier 1969). At 1200 m

elevation the beginning of flowering in different trees may vary by three months (Figs. 3A–D). No flowering occurred in a few trees in which leaves were shed during the wet season and new shoots emerged immediately thereafter (Figs. 3E, F; Reich and Borchert 1984).

TABEBUIA OCHREA SSP. NEOCHRYSANTHA (A. GENTRY) A. GENTRY, BIGNONIACEAE.—Morphology and seasonal de-

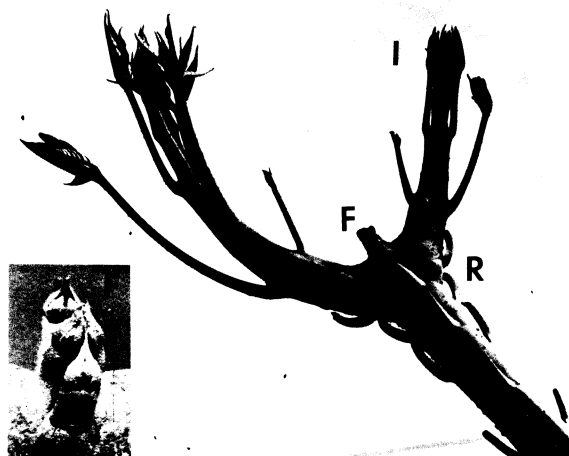


FIGURE 2. Terminal part of resting shoot of *Tabebuia rosea* with immature flower buds (F), naked vegetative buds bearing immature leaves (I), and reduced leaves between consecutive flushes (R).

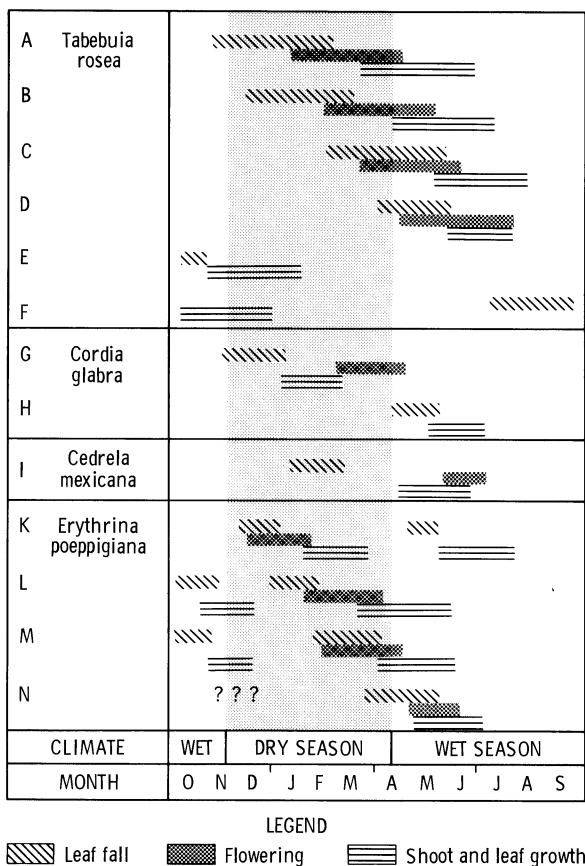


FIGURE 3. Time course of leaf fall, shoot growth and flowering in representative trees of *Tabebuia rosea*, *Cordia glabra*, *Cedrela mexicana*, and *Erythrina poeppigiana* growing in the Central Valley of Costa Rica at 1200 m altitude.

velopment of *T. ochrea* ssp. *neobrysantha* (henceforth "*T. neobrysantha*") are similar to those of *T. rosea*. The timing of development of *T. neobrysantha* in the tropical lowland deciduous forest of Guanacaste varies notably with water availability (Reich and Borchert 1982). At dry sites leaves fall early in the dry season, and irrigation or isolated rainfalls during the late dry season trigger abundant flowering of bare trees. At sites of intermediate soil moisture, trees shed their leaves slowly during the early dry season, then flower moderately during continuing drought and again after later rainfalls. At wet, riparian sites, new leaves emerge before all old leaves have fallen and no anthesis occurred during 1978. At higher elevation with modest evaporative demand, *T. neobrysantha*, like *T. rosea*, usually flowers immediately after leaf shedding.

Cordia glabra CHAM., EHRETIACEAE.—As for *Tabebuia*, the shoot system of *C. glabra* is composed of modules of

determinate growth. There is a clear distinction between the orthotropic trunk and plagiotropic lateral branches ending in terminal inflorescences which often abort before completing their development (Fig. 1B, *architectural model of Prévost*; Hallé *et al.* 1978). In the Central Valley of Costa Rica, most *C. glabra* shed their leaves during the early dry season. Leaf fall is immediately followed by the emergence of new shoots, whose growth ends with the formation of a terminal inflorescence and the subsequent opening of small, inconspicuous flowers (Fig. 3G). Fruits grow and mature during the late dry and early wet season. In two trees, leaf fall occurred during the early wet season and was followed by the emergence of new shoots whose development ended without the formation of terminal inflorescences (Fig. 3H).

CEDRELA MEXICANA ROEM., MELIACEAE.—In the Central Valley of Costa Rica, leaves of *C. mexicana* are shed during the dry season and shoot emergence occurs after the first heavy rains. Seasonal shoot growth ends with the appearance of terminal inflorescences and the opening of numerous, small flowers (Fig. 3I). Fruits grow and mature during the wet season.

ERYTHRINA POEPPIGIANA O. F. COOK, LEGUMINOSAE.—In contrast to the species discussed above, *E. poeppigiana* displays indeterminate growth on main and lateral shoots. Its large flowers are borne on axillary inflorescences (Fig. 1C; *architectural model of Attims*, Hallé *et al.* 1978). In most mature trees, leaves are shed during the early dry season and flowers open on newly formed lateral inflorescences at the distal ends of shoots. Fruits develop on leafless trees, and new shoots emerge during or after fruit maturation (Figs. 3K–M; Borchert 1980). Within the crowns of large trees, development may be asynchronous; leaves abscise and flowers develop on upper branches while lower branches retain their leaves. Many trees shed their leaves again toward the end of the wet season (October/November), but in contrast to development during the dry season this leaf fall is followed immediately by the emergence of new shoots and no inflorescences are formed (Figs. 3K–M; Borchert 1980). At 1200 m elevation, the time of anthesis ranged from January in large trees at dry sites to April in small, vigorous trees (Figs. 3K–N; Borchert 1980). Along an altitudinal gradient (950–1350 m) of decreasing evaporative demand, tree development changed from a deciduous to an evergreen pattern; deciduous trees at lower elevation flowered early in the dry season and synchronously within a population, but in evergreen trees at higher elevation asynchronous flowering occurred two to three months later.

DISCUSSION

FLOWERING IN HERBACEOUS PLANTS.—Conceptually, the

following stages of flower development can be distinguished: (I) Flower induction, *i.e.*, the process causing the transition from vegetative to reproductive development in the apical meristem; (II) Early differentiation of flower buds; (III) Development of flower buds; (IV) Anthesis, *i.e.*, the opening of flower buds and the unfolding of flowers.

For herbaceous plants, whose flower induction and development have been studied intensively (Lang 1965), progress from flower induction to anthesis is usually continuous and flowers open within a few weeks after induction. The occurrence of flower induction per se (stage I) cannot be observed directly; it is inferred from subsequent biochemical, cytological, or anatomical changes in the apical meristem (stage II). Some of these have been observed within 48 h after flower induction (Zeevaert 1976). More commonly, changes in the macroscopic structure of flower buds (stage III) appearing after vegetative plants have been exposed to a putative flower-inducing condition are used as indicators of flower induction.

While for many herbaceous plants flowering is induced by environmental stimuli, mainly photoperiod and low temperature, many plants are day-neutral, *i.e.*, they flower irrespective of environmental conditions once they have attained a certain minimum size and the ill-defined state of "ripeness to flower." In such plants the transition from the vegetative to the reproductive state is apparently determined by internal, correlative controls, not environmental triggers (Lang 1965).

FLOWERING IN TREES.—Vegetative and reproductive development are strongly interrelated in all plants, but in trees these relationships are considerably more complex than in herbaceous plants because of the structural complexity of the shoot system (Hallé *et al.* 1978), the life-long alternation between periods of active growth and periods of rest, and repeated flowering. The developmental potential of each shoot within a tree crown, and implicitly that of its apical meristem, is strongly determined by its relative position. For instance, there are long-shoots of vigorous (indeterminate) elongation growth and lateral short-shoots of limited (determinate) growth; shoots may be orthotropic (vertical) or plagiotropic (horizontal); they may be located inside or on the surface of the crown, etc. (Hallé *et al.* 1978).

Apical meristems of trees possess several developmental options (Romberger 1963). In addition to the irreversible transition from the vegetative to the reproductive mode, manifest in the formation of flower buds and bracts, there are several possible morphogenetic pathways associated with the seasonal or permanent arrest of shoot growth. A meristem may alternate between the formation of leaf primordia and bud scales or other rudimentary leaves (Figs. 2, 4), it may terminate its devel-

opment by parenchymatization or lignification, or it may abscise entirely.

The transition of a vegetative meristem to flower initiation may occur in two different, ontogenetically exclusive ways (Hallé *et al.* 1978): (i) after a period of vegetative growth the apical meristem becomes wholly transformed into a flowering axis, *i.e.*, the shoot is determinate and ends in an inflorescence (= *bipaxanth*; *e.g.*, *Cedrela*, *Cordia*, *Tabebuia*; Figs. 1A, B); (ii) the shoot apical meristem continues its vegetative activity (indeterminate growth) while producing lateral flowers or inflorescences (= *pleonanth*; *e.g.*, *Erythrina*, Fig. 1C).

In contrast to herbaceous plants, flower development in many trees is not continuous from flower induction to anthesis, but may become temporarily arrested at some intermediate stage. Final development of flower buds and anthesis will occur many months after flower initiation. This functionally important distinction has not been adequately considered in many discussions of flowering in trees. In analogy to the terminology describing development of lateral branches (*syllipsis*—continuous development of a lateral from a terminal meristem; *prolepsis*—discontinuous development of a lateral from a terminal meristem, with some intervening rest period of the lateral meristem; Hallé *et al.* 1978), I propose to distinguish between sylleptic and proleptic flowering. *Sylleptic flowering* is the continuous development of a terminal or lateral meristem into an inflorescence. *Proleptic flowering* is the discontinuous development of a terminal or lateral meristem into an inflorescence, with a rest period separating early flower development and anthesis.

Blooming of leafless, deciduous trees and anthesis during early shoot emergence are indicative of proleptic flowering. In this case, flower induction and anthesis must be controlled by two different sets of factors; these should be clearly distinguished in discussions of the timing mechanisms of flowering. For instance, while isolated rainfalls during the dry season have been clearly identified as the trigger of anthesis in many tropical proleptic tree species (Opler *et al.* 1976; Reich and Borchert 1982, 1984), the timing of flower induction and its possible controls are virtually unknown for all tropical trees and can only be inferred from an analysis of seasonal shoot growth patterns in conjunction with tree morphology.

FLOWER INDUCTION IN A TEMPERATE TREE.—As for the majority of temperate trees, but unlike many tropical species, flowers are born in apple and other rosaceous fruit trees on lateral short shoots of determinate vegetative growth (spur shoots). Seasonal development of spur shoots begins in spring with the opening of flowers and emergence of shoots preformed within the bud during the preceding growing season. Macroscopic development in spur shoots ends early in the growing season, usually in June, with the cessation of shoot elongation and the formation of

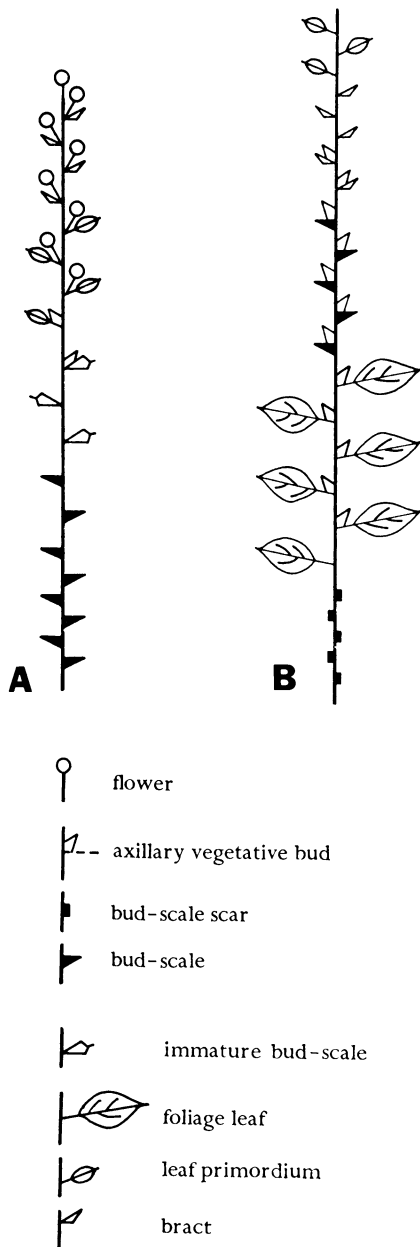


FIGURE 4. Morphogenesis of flower buds in apple (Fulford 1966). Lateral organs found (A) in a normal resting flower bud in late summer, and (B) in a bud induced by defoliation to open precociously during the summer.

bud scales enclosing the resting bud. Within this bud flowers and leaves which normally open during the next season develop after the cessation of shoot growth. Based on the series of immature organs found within the flower bud by late summer (Fig. 4A; Fulford 1966), it can be seen that the apical meristem of the spur shoot underwent

the following phase changes: from the formation of bud scales to that of leaf primordia and then flower bracts, and from the formation of vegetative axillary buds to that of axillary flower buds and finally a terminal flower bud.

Within the same apple tree, the timing of flower development varies with the position of flower buds. Flower development in terminal or axillary buds of long-shoots may be three to eight weeks later than in spur shoots (Zeller 1955). When apple trees were defoliated late in the growing season (early July) resting flower buds opened precociously, but did not produce flowers. The sequence of organs on such shoots shows that their apical meristems reverted to vegetative development after passing through the earliest stages of flower bud development, namely formation of bracts and axillary meristems (Fig. 4B; Fulford 1966). Failure of flower bud initiation in defoliated shoots has been repeatedly observed in fruit trees (Lang 1965). Similar studies combining experimental modifications of shoot growth with anatomical analysis of immature organs within the bud do not exist for tropical trees.

POSTULATED CONDITIONS INDUCIVE TO FLOWER INITIATION.—Observations for apple and other trees support the following hypothesis. For trees, the transition of apical meristems from the vegetative to the reproductive mode is determined mainly by internal, correlative factors. Flower induction and early flower development are stimulated by conditions that inhibit vegetative growth at or near the potential flower bud and favor the establishment of high carbohydrate levels in the inducible meristem.

Observations with tropical trees are in agreement with this hypothesis, based originally on manipulations of shoot growth in fruit trees and recently restated as the "Nutrient Diversion Hypothesis" by Sachs (1977). Similar hypotheses were originally proposed to explain flower induction in herbaceous plants (Klebs 1913). At present, available evidence suggests that carbohydrate levels as well as the balance between plant growth regulators in vegetative buds are involved in the control of flower induction (Hackett and Sachs 1967, Zeevaart 1976, Tran Thanh Van 1980). In view of the very small number of descriptive and experimental studies of flower induction in trees (Kozłowski 1971), any generalization should be considered tentative.

The combination of factors establishing conditions favorable for flower initiation and development varies with the species-specific position of the inflorescence within a tree's branch system and with the seasonal pattern of vegetative and reproductive growth. Flower induction in hapaxanthic and pleoanthic species therefore will be considered separately.

INDUCTION OF TERMINAL INFLORESCENCES IN TROPICAL TREES.—In shoots of determinate growth bearing a ter-

minal inflorescence, *e.g.*, in spur shoots of apple and other rosaceous fruit trees and in the "modules" of *Tabebuia*, *Cordia*, and many other hapaxanthic tropical trees (Figs. 1A, B; Hallé *et al.* 1978, see models of Leeuwenberg, Koriba, Prévost, Petit and others), the cessation of shoot growth is caused by correlative inhibition and usually occurs under environmental conditions favorable for plant growth. The arrest of shoot growth eliminates a principal sink for the assimilates produced by mature leaves and is likely to cause a rising carbohydrate level in the shoot. Based on macroscopic observations of terminal buds it has been suggested that flower initiation regularly follows shoot growth cessation in hapaxanthic species (Hallé *et al.* 1978), *i.e.*, it is caused by endogenous, not environmental factors. If generally true, this observation would also imply that the absence of anthesis, as described above for *Tabebuia* and *Cordia* with abnormal periodicity of vegetative growth, must be due to abortion of the inflorescence or to incomplete development of flower buds (*Tabebuia*: Fig. 2). In some modular species of the Apocynaceae, the apical meristem may undergo parenchymatization instead of flower initiation (J. Fisher, pers. comm.).

INDUCTION OF LATERAL INFLORESCENCES IN TROPICAL TREES.—

For pleonanthic species the relation between shoot growth and lateral flower development is less direct than for hapaxanthic trees, and little information on the control of flower initiation can be gained from analyzing shoot morphology or the time course of vegetative growth.

Indeterminate shoot growth of mature, temperate trees ceases before the end of the growing season and is probably under endogenous control (Wareing 1956, Borchert 1978). Similarly, extension growth in tropical deciduous trees is limited to a few weeks during the early wet season (Daubenmire 1972). For *Erythrina* it is usually completed within a few weeks after shoot emergence, irrespective of prevailing environmental conditions (Figs. 3K–N). It is not known, in the case of proleptic tropical trees like *Erythrina*, whether flower initiation in the axillary buds of newly formed shoots takes place shortly after the cessation of seasonal shoot growth as in many temperate species (*e.g.*, *Acer pseudoplatanus*, Anderson and Guard 1964, Kozlowski 1971) or just prior to the final development of the inflorescence. For *Erythrina* and *Tabebuia*, flowering follows leaf fall only during the dry season (Fig. 3). This suggests that water stress contributes to the establishment of internal conditions conducive to flowering, possibly by inhibiting shoot emergence. It is not known which stage of the flowering process is inhibited in the non-flowering trees changing leaves during the wet season (Figs. 3E, F, H, K–M).

The type of experimental study needed to advance our understanding of flower induction in tropical trees is illustrated by the following work on mango (*Mangifera*

indica; Reece *et al.* 1946). Flowering in mango is hapaxanthic as described above for *Cordia* and *Cedrela*. If the terminal bud containing the developing inflorescence is removed, axillary buds in the distal region of the shoot, which normally form vegetative lateral shoots, develop into inflorescences; flower initiation is induced by a change in growth correlations within the shoot. If prior to decapitation all leaves are removed on the distal end of the shoot and the shoot is ringed (phloem interrupted) below the defoliated part, only vegetative lateral shoots are formed. Defoliation and ringing four days after decapitation permit formation of lateral inflorescences. One might infer that under conditions of good carbohydrate supply flowers were induced within four days. However, if a single leaf remains on the decapitated, ringed, and defoliated shoot, all lateral buds produce inflorescences, an observation that points to a role of growth regulators in flower induction of trees (Lang 1965).

In conclusion, flower induction in tropical trees appears to be mainly under endogenous control and affected by environmental factors only indirectly through their effect on seasonal vegetative development of trees. This view is supported by the fact that most trees must pass through a prolonged juvenile period before acquiring the potential to flower and, once mature, often do not flower every year, a phenomenon well documented for tropical trees (Koelmeyer 1959, Bullock and Bawa 1982).

Contrary to repeated claims in the ecological literature (*e.g.*, Janzen 1967, Frankie *et al.* 1974, Opler *et al.* 1976, Stiles 1978), there is no good evidence for the direct control of flowering in tropical trees by short photoperiods. Coffee (*Coffea arabica*) flowers are initiated under all photoperiods occurring in the tropics, but not under 14 h or more of daylight (Piringer and Borthwick 1955). For *Plumeria acumenata* (as for many other juvenile, tropical or temperate trees) short photoperiods induce shoot growth cessation (Wareing 1956, Longman and Jenik 1974, Stubblebine *et al.* 1978) while shoots exposed to long photoperiods may grow continuously; in the case of *Plumeria*, they do not flower (Lawton and Akpan 1968). These observations of suppression of flowering by long photoperiods do not prove, however, that flowers are induced by short photoperiods. Finally, for the subtropical woody vine *Bougainvillea*, development of the immature flower primordia, not flower induction, can be stimulated by growth retardants, high light intensity, or short photoperiods (Hackett and Sachs 1966, 1967).

CONTROL OF ANTHESIS IN TROPICAL TREES.—Virtually all successful attempts to establish good temporal correlations between environmental changes and phenological data on synchronous flowering in many trees deal with the triggering of anthesis in proleptic species, not with flower induction. The proleptic flowering habit apparently prevails among both tropical and temperate deciduous trees

adapted to strongly seasonal climates, but it is manifest also in many tropical rainforest canopy trees which bloom when leafless.

The control of anthesis is basically different from that of flower induction. While the latter implies a switch from vegetative to reproductive development, *i.e.*, a basic redirection of morphogenesis in the apical meristem, the triggering of anthesis mainly involves release from an inhibitory endogenous or environmental condition, usually water stress or low temperature, which prevents flower buds from completing their development.

For temperate trees, and probably for most proleptic tropical trees, anthesis, like expansion of early leaves in a flush, consists essentially in the expansion of flower parts preformed in the resting bud. Available evidence suggests that for most tropical trees anthesis is primarily, if not exclusively, prevented by water stress within the tree crown (Reich and Borchert 1982, 1984). Cell expansion is known to be suppressed by even moderate water stress (water potentials of <-0.5 MPa or <-5 bar; Larcher 1980). For fully foliated trees, daily water deficits resulting from transpiration apparently suppress opening of large flowers. The observation that most sylleptic flowers (*e.g.*, *C. glabra*, *C. mexicana*) and flowers of evergreen trees (Bawa and Opler 1975) are small and inconspicuous supports this idea.

Leaf fall occurring in moderately water-stressed trees eliminates tree water deficits and triggers anthesis during continuing drought (*e.g.*, *T. neobrysantha*, *Cochlospermum vitifolium*; Reich and Borchert 1982, 1984). In these cases the timing of anthesis is thus a function of the timing of leaf fall, which varies with leaf age, leaf structure (mesomorphic vs xeromorphic leaves), and environmental conditions (Reich and Borchert 1984). Various combinations of factors determining leaf fall may cause variations of four to five months in the timing of leaf fall and hence of anthesis in the following species: *C. vitifolium* (Fournier and Salas 1966), *E. poeppigiana* (Figs. 3K–N, Borchert 1980), *T. rosea* (Figs. 3A–D; Fournier 1969, Frankie *et al.* 1974), and *T. neobrysantha* (Reich and Borchert 1982). In general, anthesis caused by leaf fall is likely to be highly asynchronous within a population (“cornucopia” blooming pattern described by Gentry 1976). Most likely, flowering triggered by leaf fall is reflected in the first peak of dry season flowering observed by Fournier and Salas (1966) in a tropical montane forest subject to moderate seasonal drought. Similarly, many evergreen trees in tropical rain forests and at riparian sites of deciduous forests flower during periods of moderate drought after having shed a major part of their foliage (Daubenmire 1972, Frankie *et al.* 1974, Mori and Kallunki 1976, Alvim and Alvim 1978, Stiles 1978). For the evergreen coffee tree, anthesis is induced by rainfall or irrigation restoring a favorable water balance in water-stressed trees (Piringer and Borthwick 1955, Alvim 1960).

At dry sites, where leaf shedding is not sufficient to balance the water economy of water-stressed deciduous trees, rainfall of adequate intensity causes rehydration of trees and subsequent highly synchronous anthesis (“big bang species” of Gentry 1976, Opler *et al.* 1976, Augspurger 1980, Reich and Borchert 1982). Apparently, most tree species will flower whenever they achieve a positive water balance, often twice during the same dry season (Opler *et al.* 1976, Reich and Borchert 1982). This indicates that prior to anthesis buds are not “dormant,” but in a state of rest or “drought-imposed dormancy,” analogous to the state of “cold-imposed dormancy” in buds of temperate trees in which “true” dormancy has been broken by low temperature exposure (Kramer and Kozlowski 1979). Similarly, for hapaxanthic, sylleptic species, rehydration following leaf fall (*C. glabra*, Fig. 3G) or rains (*C. mexicana*, Fig. 3I) causes a flush of shoot growth which ends with flowering.

In the temperate zone, anthesis of most proleptic species is caused by rising temperatures in spring. Similarly, at the northern end of the range of Central American tree species such as *C. vitifolium* and *T. rosea*, anthesis appears to be delayed by low winter temperatures and occurs in March/April (Janzen 1967; P. V. Wells, pers. comm.). Triggering of anthesis by changing photoperiod has not been reported in the literature.

EVOLUTION OF TEMPORAL FLOWERING PATTERNS.—In view of the strong interrelation between tree architecture, vegetative growth, and flower development, the adaptive value of flowering behavior of tropical trees should not be considered separately. It should be considered only within the context of an analysis of the adaptive geometry of a tree species, its development, and its interaction with the environment. Considering our rudimentary understanding of the adaptive significance of the wide variety of architectural models encountered among tropical trees (Hallé *et al.* 1978, Borchert and Slade 1981), it appears premature to explain flowering patterns associated with these architectural models separately in evolutionary terms. Current discussions of temporal flowering patterns in tropical trees constitute typical examples of the widespread tendency to break organisms conceptually into separate units and to propose “adaptive stories” for each. This procedure was recently criticized by Gould and Lewontin (1979) and contrasted with the need to analyze organisms as integrated units, as postulated above and attempted by Opler (1978) for trees.

Apart from the basic problem of ignoring the relations of flowering to other aspects of tree development, most recent discussions of flowering in tropical trees contain one or the other of the following inaccuracies or misunderstandings: (i) no distinction is made between flower induction and anthesis, and (ii) the separation in time between these two processes in proleptic flowering

is ignored; (iii) short photoperiods are postulated as triggers of flower induction or anthesis in spite of the lack of sound evidence of photoperiodic control of flowering in trees; (iv) the coincidence between dry season and short photoperiods, and (v) the role of tree water status in the control of anthesis is ignored; and (vi) proximate and ultimate causes are confused and causal and evolutionary reasoning are mixed.

Like all other aspects of tree development, the phenology of flowering is determined partly by genetic, partly by environmental factors. For instance, hapaxanthly vs pleoanthy and syllepsis vs prolepsis appear to be largely genetically fixed and determine the timing of flower development and anthesis relative to a tree's seasonal vegetative development. Thus, if the opening of flowers in leafless deciduous trees is considered to be necessary or advantageous for successful pollination, then one might argue that the proleptic habit has been selected for in deciduous trees. However, the actual timing of anthesis, as relevant in discussions of the adaptive significance of "staggered" flowering, depends on the timing of a tree's vegetative development, particularly leaf fall. This is determined by environmental constraints and not by biotic factors such as pollinator availability. The variation in peak flowering of seasonal, tropical forests as a function of the severity of drought (Fournier and Salas 1966, Janzen 1967), flowering during drought periods in tropical

rain forests, and the wide temporal range of flowering within individual species as a function of tree water relations (see above) suggest a predominant role of seasonal changes in water status as determinants of tree development including flowering (Reich and Borchert 1984). Considering the environmental constraints imposed upon tree development and the long generation time of trees as compared to the short generation time of their principal pollinators, insects, any temporal correlation between flowering and insect activity is more likely to have resulted from adaptation of insect life cycles to seasonal tree development than from coevolution between trees and insects.

It should be noted that the above discussion pertains to tropical trees and forests subject to temporary environmental stress, as imposed by the prolonged dry season on the Pacific slope of Costa Rica or the irregular, but widespread, dry spells in tropical rain forests. It does not necessarily contradict the suggestion that the regularly spaced timing of flowering among plants of different life forms, as documented by Stiles (1978) for a tropical rainforest, might reflect selection for optimal plant-pollinator interaction.

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