

15

Phenological Responses to Seasonality in Tropical Forest Plants

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Tropical rainforests include more plant species than any other habitat (Gentry, 1988). An unmatched variety of phenological patterns contributes to this diversity. This variety is illustrated by the one tropical forest for which the reproductive phenologies of most plants are known. On Barro Colorado Island, Panama, most species flower and fruit during short, predictable periods; still more than 600 species have been recorded in flower and in fruit during each calendar month (Croat, 1975, 1978).

Two largely independent research disciplines have sought explanations for the wide variety of phenological patterns observed among tropical forest plants. Ecologists have studied biotic interactions that select for timing (Janzen, 1967; Bawa, 1983). Examples include seasonal changes in levels of herbivory, pollination, seed predation, and seed dispersal. Physiologists, on the other hand, have studied abiotic factors that limit plants or cue plant responses (Schimpfer, 1903). Examples include wetting after drought, changes in photoperiod, sea-

sonal changes in temperature, and short-term changes in temperature associated with heavy rainfall or invasions by cold air masses (Njoku, 1963; Wycherley, 1973; Opler, Frankie & Baker, 1976; Buttrose & Alexander, 1978; Ashton et al., 1988). A number of environmental factors that influence the phenologies of tropical forest plants have been identified. The approach has been to study single factors, however, and an integrative understanding of tropical forest plant phenologies has yet to emerge.

The control of plant phenology in tropical forests is of practical interest because deforestation is rapidly changing tropical landscapes and modifying tropical climates, which may in turn disrupt the phenologies of tropical forest plants. Forest evapotranspiration contributes to high tropical rainfall (Salati et al., 1979), and global climate models predict that deforestation will diminish rainfall and intensify tropical seasonality (Shukla, Nobre & Sellers, 1990). On a smaller scale, deforestation changes environmental conditions in surviving forest patches (Kapos, 1989). Changing tropical climates may soon disrupt the mechanisms that control the timing of plant production and alter interactions among species. The potential consequences are illustrated by the frequent failure of introduced agricultural crops when the mechanisms that control timing fail in a new environment, and critical life history events occur at the wrong time (Evans, 1980).

The purpose of this article is to review the seasonality of tropical forests, to identify environmental factors that vary seasonally and have consistent effects on plants, and to integrate those factors to predict the timing of leaf production and flowering. A clear distinction will be drawn between the proximate cues of plant phenologies and the ultimate selective factors that have shaped phenologies over evolutionary time. The timing of fruit maturation and seed dispersal will not be considered due to the additional complications imposed by germination and seedling requirements. As an example, more than 200 plant species delay fruit maturation by at least one full season after flowering on Barro Colorado Island (Croat, 1975), presumably so that dispersal coincides with conditions that are optimal for seedling establishment (Garwood, 1983).

15.1 TROPICAL FOREST SEASONS

The movements of the intertropical convergence zone (ITCZ) influence seasonality over large parts of the tropics (Hastenrath, 1985). The ITCZ develops when air warmed by the zenithal sun rises and

cools adiabatically to form clouds and rain. Outside the ITCZ, the surface tradewinds rush to replace air rising within the ITCZ, and cloud cover and rainfall are reduced. The ITCZ moves latitudinally some two months after the zenithal sun, and its movements bring wet and dry seasons to large parts of the tropics. Rainfall, cloud cover, irradiance, atmospheric saturation deficits, windspeed, and potential evapotranspiration all covary seasonally. In addition to direct effects on plant growth, these seasonal patterns may affect populations of animals and microbes that interact with plants. As a consequence, most tropical forest plants experience simultaneous seasonal change in several environmental factors. These environmental factors will now be grouped into four broad classes, and evidence of their effects on tropical forest plant phenologies will be evaluated.

15.1.1 Moisture availability

In many tropical forests, low dry-season rainfall reduces moisture availability just as increases in atmospheric saturation deficits, irradiance, and leaf temperatures increase transpirational demand. The resultant moisture shortfalls are a primary determinant of tropical vegetation types.

Evergreen forests predominate where rainfall exceeds evapotranspiration for 11 or 12 months (Köppen, 1936; Medina, 1983; Whitmore, 1984). Plant water deficits have been recorded in evergreen tropical forests both during unusual drought events and also as an adaptive response to high irradiance (Chiariello, Field & Mooney, 1987; Oberbauer, Strain & Riechers, 1987). Predictable seasonal water deficits are absent from most tropical evergreen forests, however, and moisture seasonality is unlikely to be an important factor influencing plant phenologies (Frankie, Baker & Opler, 1974; News-trom et al., 1994).

Semideciduous tropical forests occur where rainfall exceeds evapotranspiration for eight to 10 months (Köppen, 1936; Medina, 1983; Whitmore, 1984). Dry-season drought is predictable in semideciduous forests, and in some years, plant moisture stress can be severe (Leigh et al., 1990; Wright et al., 1992; Condit, Hubbell & Foster, 1995). Nonetheless, many plants maintain year-round growth. For example, 90% of the plant species are evergreen and 20% of the plant species flower, fill, and disperse fruit during the four-month dry season on Barro Colorado Island, Panama (Croat, 1975, 1978). Moisture sea-

sonality is only likely to be an important factor influencing the phenologies of drought-sensitive species in semideciduous forests (Reich & Borchert, 1984; Wright & Cornejo, 1990a,b; Wright et al., 1992).

In contrast, deciduous tropical forests predominate where evapotranspiration exceeds rainfall for five or more months (Köppen, 1936; Medina, 1983; Whitmore, 1984). Dry-season water deficits are potentially severe, and the dominant phenological pattern is to avoid dry-season water stress by becoming deciduous during the dry season (Frankie, Baker & Opler, 1974; Lieberman & Lieberman, 1982; Bullock & Solis-Magallanes, 1990). Deciduous species may renew growth during the dry season, but constraints imposed by water deficits are again evident. For example, many deciduous species flower after a heavy dry-season rain (Opler, Frankie & Baker, 1976). More perplexing are deciduous species that renew growth under continuous drought. Reich and Borchert (1982, 1984, 1988) hypothesized that these species experience water stress early in the dry season because senescent leaves have lost the ability to control transpiration. As a consequence, leaf abscission occurs before soil water is completely depleted, and the leafless tree is able to take up water and renew growth under continuous drought.

At this time, predictions of the relationship between phenology and water stress for deciduous and semideciduous forests depend on species-by-species information on adaptations for drought resistance (Reich & Borchert, 1984; Borchert, 1994). The possible adaptations are few in number (Jones, Turner & Osmond, 1981). Transpirational water loss can be reduced through reductions in leaf area, cuticular conductance, and leaf temperatures via reductions in the amount of radiation absorbed. Water uptake can be maintained through deep, extensive root systems and low resistances to xylem water flow. Tissue tolerance to moisture stress can be enhanced through increases in tissue osmotic concentrations and the rigidity of cell walls. These mechanisms of drought resistance have all been observed among tropical forest plants (Medina, 1983). The critical question here is whether growth is possible during the drier season, as growth and cell expansion are among the first plant processes to be adversely affected by small water deficits and reductions in tissue turgor pressures (Bradford & Hsiao, 1982).

Most tropical deciduous forests include a few evergreen plants (Frankie, Baker & Opler, 1974; Lieberman & Lieberman, 1982; Bullock & Solis-Magallanes, 1990). In contrast to their deciduous neighbors, evergreen species maintain positive leaf turgor potentials in the dry season (Sobrado, 1986; Fanjul & Barradas, 1987). Similar dry-

season reductions in osmotic potentials occur in both deciduous and evergreen species, however, evergreen species have deep root systems and inelastic cell walls relative to their deciduous neighbors (Sobrado & Cuenca, 1979; Sobrado, 1986; Fanjul & Barradas, 1987). Deep root systems also characterize evergreen trees in tropical savannahs (Sarmiento, Goldstein & Meinzer, 1985). A few deciduous forest species may even reverse the normal pattern of leaf phenology. For example, the shrub *Jacquinia pungens* is deciduous in the wet season and foliated in the dry season in the deciduous forests of Mesoamerica (Janzen, 1972). The depth of the root system may again be critical. The deep tap root of *J. pungens* is exceptional for a deciduous forest shrub and allows the maintenance of high dry-season water potentials (Fanjul & Barradas, 1987; Janzen, 1972; Oberbauer, 1985). Recent data for trees from semideciduous and deciduous tropical forests suggest that analyses of hydraulic architecture and consequent dry-season water relations can predict phenologies (Borchert, 1994; Machado & Tyree, 1994; Tyree & Ewers, Chapter 8).

15.1.2 Light

Most tropical forests experience substantial seasonal variation in irradiance. In the wet tropics, global radiation averages 50% greater in the highest month than in the lowest month [compiled for the 24 tropical sites with annual rainfall > 1000 mm in Müller (1982)]. Seasonal changes in cloud cover, daylength and solar elevation contribute to seasonal variation in irradiance (Chazdon & Fetcher, 1984; Chazdon et al., Chapter 1). The importance of day length and solar elevation increase with latitude, and the month of maximum global radiation falls close to the summer solstice at higher latitudes within the tropics (Figure 15.1). The quantitative importance of cloud cover can be illustrated by a comparison of the equinoxes for a 17-year record from central Panama (Windsor, 1990). Global radiation averages 31% greater on the March equinox when dry-season conditions with negligible cloud cover prevail. Cloud cover increases toward the equator (Hastenrath, 1985), and within 10° of the equator, the month of maximum global radiation is less tightly constrained by solar elevation (Figure 15.1) and reflects the local seasonality of cloud cover.

Predictable seasonal changes in light levels will be a potent selective agent on the phenologies of light limited plants. Light limits many tropical forest plants. Photosynthetically active radiation (PAR) in the shaded understory of tropical forests is as low as in any other habitat

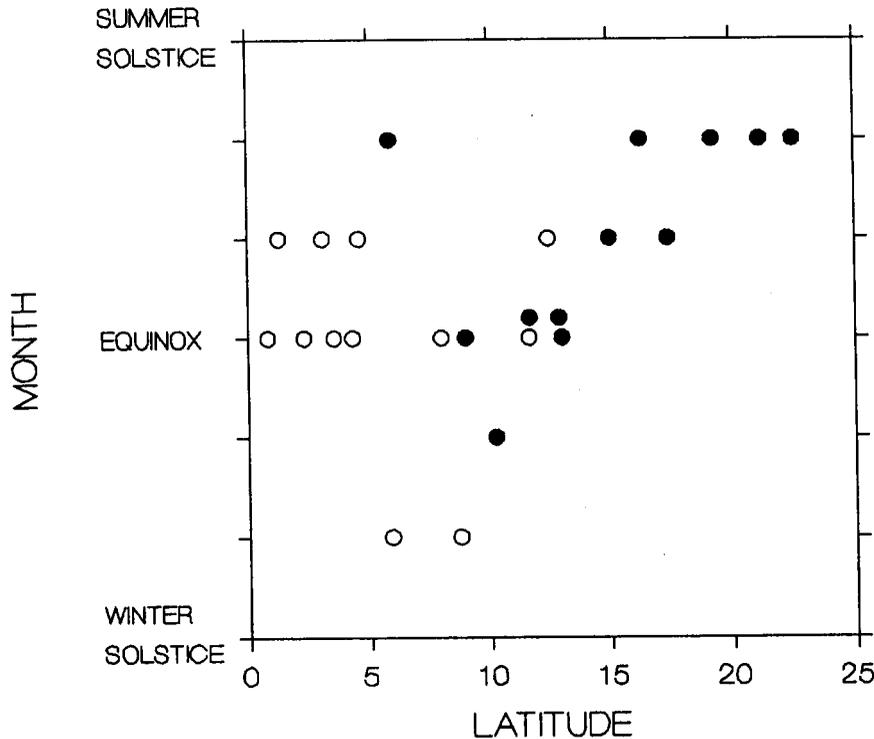


Figure 15.1. The relation between latitude and the month of maximum global radiation within the wet tropics. Closed and open symbols represent sites where the ratio of maximum to minimum mean monthly global radiation is above and below the median for the wet tropics, respectively. Annual rainfall was greater than 1000 mm at all sites. Data compiled from Müller (1982) and Windsor (1990).

occupied by autotrophic plants (Björkman & Ludlow, 1972). The growth of understory plants increases dramatically in response to short sunflecks that pass through small openings in the canopy (Pearcy, 1983) and after treefalls open the canopy overhead (Brokaw, 1985; Fisher, Howe & Wright, 1991).

Light may also limit taller plants. Radiant energy is extinguished exponentially with distance beneath forest canopies (Kira, Shinozaki & Hozumi, 1969). Above-canopy PAR was reduced by 94% just 5 m into the canopy of a wet forest in Puerto Rico (Johnson & Atwood, 1970), and global radiation was reduced by 53% just 6 m into the canopy of a Malaysian rainforest (Aoki, Yabuki & Koyama, 1975; Yoda, 1974). PAR is extinguished more rapidly than global radiation

due to differential absorption by leaves. Limiting levels of PAR predominate directly below the uppermost leaves of tropical forests (Chazdon et al., Chapter 1).

Correlations between plant performance and irradiance suggest that tropical forest trees are light limited. The radial growth of trees from evergreen forests increases with irradiance in Surinam and possibly Costa Rica (Schulz, 1960; Clark & Clark, 1994). Seed set increases with irradiance for several trees in Borneo (Wycherley, 1973), and the likelihood of a mast flowering increases with irradiance in peninsular Malaysia (Van Schaik, 1986). These correlations are consistent with limitation by irradiance, but shifts in allocation and effects of covarying environmental factors cannot be discounted.

Physiological measurements provide stronger evidence that light limits tropical trees. Light often limits photosynthesis by canopy leaves. Canopy leaves measured *in situ* become saturated with light at photosynthetic photon flux densities (PPFD) of 450 to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for trees from a wide variety of tropical forests (Oberbauer & Strain, 1986; Pearcy, 1987; Zotz and Winter, Chapter 3). Lower light levels will limit photosynthesis. PPFD varied by three orders of magnitude and limited photosynthesis in most determinations made between 0800 and 1000 h for leaves from above 29 m in an Australian rainforest tree. PPFD was less than 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 71% of diurnal course measurements for canopy leaves of *Pentaclethra maculosa* in an evergreen forest in Costa Rica (Oberbauer & Strain, 1986). Low light levels associated with heavy cloud cover often limit photosynthesis by the emergent tree *Ceiba pentandra* during the wet season in central Panama (Zotz & Winter, Chapter 3). Self shading, lateral shading by neighbors, and shading by competing lianas affect all but the uppermost leaves in tropical forests, and light interception by clouds affects all leaves. Thus, predictable, seasonal changes in irradiance may be an important selective agent on the phenologies of tropical forest plants.

15.1.3 Biotic interactions

Seasonal changes in the activities of interacting animals and microbes also influence tropical forest plant phenologies. Possibilities include selection to coincide with the seasonality of mutualists, such as pollinators, and selection to avoid the seasonality of pests, such as seed predators and herbivores. Many tropical forest animals specialize on particular host plant or on a small group of related host plants

(Janzen, 1980; Frankie et al., 1983). It is well established that host specialists can cause strong selection on plant phenologies (Augspurger, 1981). However, specialists must track the seasonality of their hosts, and stabilizing selection or directional selection for earlier or later production may result depending on the autecologies of the particular species involved (Wright, 1990; Van Schaik, Terborgh & Wright, 1993). Host specialists are unlikely to have consistent, predictable effects on plant phenology.

Consistent effects are more likely when a variety of host generalists share a common seasonality. For example, in seasonal tropical forests, many herbivorous insects are inactive or restricted to moist microsites during the drier season (Janzen, 1973; Wolda, 1978). This shared seasonality creates the potential for phenological selection.

This potential will be illustrated by a comparison of seasonal changes in leaf herbivory across three tropical forests with very different seasonalities. Tropical forest is near its distributional limit in the Accra Plains of Ghana where rainfall seasonality is extreme. Insect herbivory was largely restricted to the wet season at this site, and strong selection for dry-season leaf production resulted (Lieberman & Lieberman, 1982). The seasonal fluctuations of herbivorous insects decrease in tropical forests with milder dry seasons (Wolda, 1988). Relative to Accra, seasonal changes in herbivory were modest in the semideciduous forests of Barro Colorado Island, Panama, averaging 20–22% in the three driest months and 25–42% in the nine wetter months (Aide, 1988). Finally, seasonal changes in herbivory were absent for an understory shrub in the evergreen forests of La Selva, Costa Rica (Marquis, 1987). The potential for selection by seasonal insect populations increases with rainfall seasonality. Less is known about seasonal changes in tropical forest microbes, but a similar pattern is to be expected (G. Gilbert, personal communication).

15.1.4 Mineral nutrients

Temporal variation in nutrient availability has been documented for several tropical forests. Pulses of high nitrogen and phosphate availability are often associated with rapid changes in moisture availability that cause lysis of soil and litter microbes (reviewed by Lodge, McDowell & McSwiney, 1994). Microbial death simultaneously frees nutrients and reduces microbial competition for those nutrients. The type of change in moisture availability that induces microbe death varies among forests. Microbe death is caused by droughts in normally

aseasonal, everwet forests, and by the rapid increase in moisture availability at the beginning of the wet season in monsoonal and other seasonally dry forests.

There may also be long-term seasonal changes in nutrient availability that are unrelated to rapid changes in moisture availability. Magnesium and calcium availability increased steadily throughout the wet season, reached their annual peak in the final month of the wet season, and then crashed rapidly to low dry-season levels for three consecutive years on Barro Colorado Island (Yavitt & Wright, unpublished data). This seasonal pattern of availability may characterize nutrients whose concentrations remain high in recalcitrant litter fractions until final release from decayed litter (Cornejo, Verala & Wright, 1994). Other nutrients that are released more rapidly during decomposition had different seasonal patterns on Barro Colorado Island. Phosphate and ammonium increased in the dry season then decreased in the wet season, while potassium and sulfate did not vary seasonally. Likewise, phosphate and ammonium availabilities did not vary among months in the relatively aseasonal, evergreen forests of La Selva, Costa Rica (Vitousek & Denslow, 1986).

Predictable changes in nutrient availability, like those outlined above, may select for plant phenologies. Many wild plants are able to store and recycle nutrients effectively (Chapin, 1980); however, this would tend to minimize the impact of temporal variation in nutrient availabilities. Perhaps for this reason the potential effect of temporal variation in nutrient availability on plant phenologies has generally been overlooked.

15.2 SEASONALITY AND PHENOLOGY

Seasonal changes in moisture availability, irradiance, and insect activity can be expected to have consistent effects on large numbers of plant species in seasonal tropical forests. These three factors will often covary, with the drier season having higher irradiance and reduced insect activity. We have yet to integrate the potential effects of these three factors in order to predict tropical forest plant phenologies.

Rainfall seasonality will take precedence over other seasonal changes whenever water deficits are sufficient to arrest plant cell expansion and growth (Reich & Borchert, 1984). Given adequate water supplies, selection will favor leaf production during seasons of low herbivore activity and high irradiance. This will be true because most herbivory occurs in the first month of leaf life before leaves

become fully lignified and also because photosynthetic capacities decline with age once leaves complete expansion (Coley, 1980; Wright & Van Schaik, 1994). Flowering will be selected to coincide with maximum photosynthesis because it is energetically most efficient to transfer assimilates directly to growing organs rather than to store them in different tissues first and to mobilize and translocate them later (Chapin, Schulze & Mooney, 1990; Wright & Van Schaik, 1994). Thus, there are two general predictions. First, plants without dry-season water supplies must produce leaves and flowers in the wet season (Reich & Borchert, 1984). Second, when water is available, selection will favor leaf and flower production in seasons when irradiance is high and herbivory is low (Wright & Van Schaik, 1994). Specific predictions will vary with site seasonality and plant drought sensitivity.

In evergreen tropical forests, where moisture deficits are absent or occur irregularly and fluctuations in herbivore pressure are modest, the timing of leaf and flower production is predicted to coincide with peak irradiance. This hypothesis was tested for four evergreen forests where minimum mean monthly rainfall was greater than 60 mm (Wright & Van Schaik, 1994). On average, twice as many tree species as expected by chance centered leaf and flower production on the three sunniest months in evergreen forests from Central America, the Guyana shield, central Amazonia and Atlantic coastal Brazil (Figure 15.2). This result is consistent with the hypothesis that tree phenologies have been selected to coincide with peak irradiance (Wright & Van Schaik, 1994).

Specific predictions for more seasonal forests must incorporate an independent assessment of dry-season access to water. Such an analysis was possible for monsoon forests from East Java, where roots were excavated, and for deciduous and semideciduous forests from Venezuela and Panama, where dry-season tissue water potentials were measured (Coster, 1932; Sobrado, 1986; Wright & Van Schaik, 1994). Irradiance peaked in the dry season in all three forests, and 12 of the 17 species with access to dry-season water supplies concentrated leaf and flower production in the dry season. In contrast, the 15 species with limited access to dry-season water all concentrated leaf and flower production in the wetter season (Wright & Van Schaik, 1994). Additional evidence that water stress limits leaf and flower production in deciduous and semideciduous tropical forests was reviewed in section 15.1.1.

Dry-season peaks in irradiance and dry-season lows in pest activity will both select for dry-season leaf and flower production in most

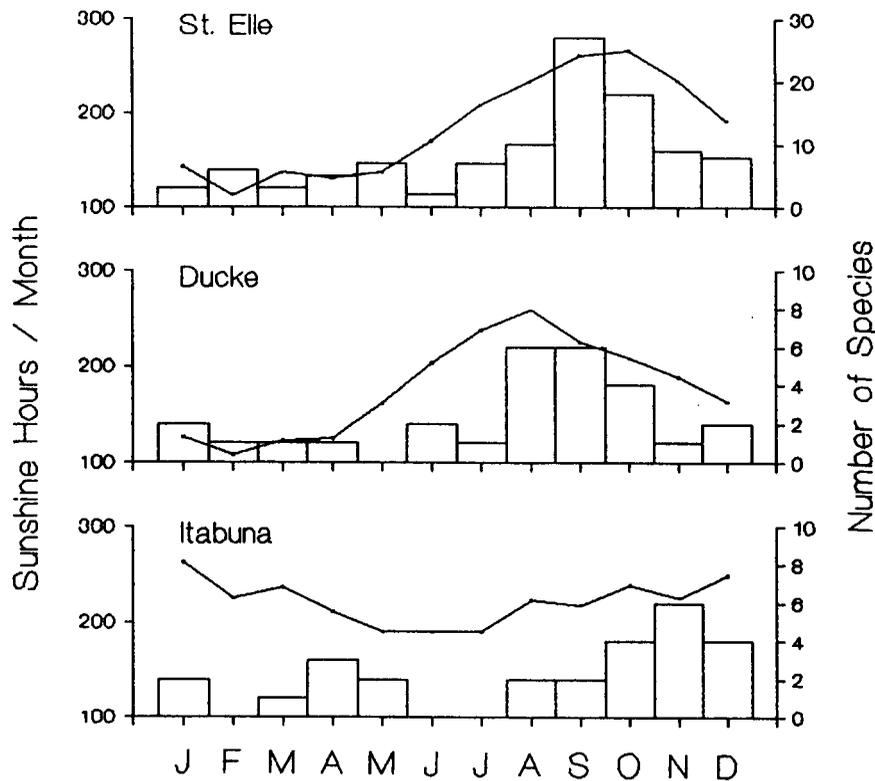


Fig. 15.2. The relation between flowering and sunshine for three evergreen tropical forests. The solid line represents mean numbers of sunshine hours for each month. The histogram represents numbers of tree species in flower. Flowering data for St. Elie, French Guyana; Ducke, Brazil; and Itabuna, Brazil from Sabatier (1985), Alencar et al. (1979), and Alvim and Alvim (1978), respectively. Sunshine hours taken from these sources or from standard meteorological references (see Wright & Van Schaik, 1994).

seasonal tropical forests. The seasonal forests of Makakou, Gabon, offer an opportunity to evaluate the relative importance of seasonal changes in insect abundance and irradiance. Insect biomass follows the expected seasonal pattern at Makokou and averages 3.9 times greater in the wet season. The three dry months are exceptionally cloudy, however, and the number of sunshine hours actually averages 2.1 times greater during the wetter months (Charles-Dominique, 1977). More than 95% of the tree and liana species examined at Makakou concentrated leaf and flower production during the wetter, sunnier months, and the dry-season peak of leaf and flower production

characteristic of other tropical forests with a three-month dry season was absent (Hladik, 1973, 1978; Charles-Dominique, 1977). The Makokou forest phenologies are also consistent with the hypothesis that seasonal patterns of irradiance have been an important selective agent on tree seasonality in tropical forests.

Specific predictions are also possible for plant life forms for two reasons. First, there are consistent differences in rooting depths among life forms. Mean maximum rooting depths are less than 20 cm for mature herbs, between 30 and 90 cm for mature shrubs, between 70 and 120 cm for 2 m to 3 m tall tree saplings, and potentially much deeper for mature canopy trees and lianas on Barro Colorado Island, Panama (Becker & Castillo, 1990; Mulkey, Smith & Wright 1991; Wright et al., 1992; personal observation). All else equal, dry-season water deficits should be maximal among understory herbs, intermediate among shrubs, and least for mature trees and canopy lianas. A second difference among plant life forms that might contribute to differences in phenologies concerns irradiance seasonality at sites with significant seasonal changes in cloud cover. Cloud cover scatters and reduces direct beam radiation and increases diffuse radiation. Cloud cover will cause large reductions in PAR in the canopy, where direct beam radiation is important, and smaller reductions in PAR in the understory, where diffuse radiation is more important (Björkman & Ludlow, 1972). All else equal, understory herbs and shrubs should experience relatively modest dry-season increases in irradiance, while canopy trees and lianas should experience large dry-season increases in irradiance. Both rooting depths and irradiance seasonality lead to the prediction that selection for dry-season production should be weakest among understory herbs, intermediate among understory shrubs, and strongest for canopy trees, and lianas. On Barro Colorado Island, Panama, the proportion of forest species that concentrate both flowering and fruit maturation in the dry season is least for understory herbs and greatest for trees, as predicted (Table 15.1).

15.3 PROXIMATE CUES

The proximate cues that initiate plant production may differ from the ultimate selective factors. For example, photoperiod is an excellent predictor of freezing winter temperature at higher latitudes, and photoperiod is the proximate cue for the phenologies of many temperate zone plants even though potential damage from freezing is the

Table 15.1. The number of forest herb, shrub, and tree species that flower and disperse fruit in the same season on Barro Colorado Island, Panama. Data compiled from Croat (1987).

	Season	
	Dry	Wet
Herbs	3	33
Shrubs	5	21
Trees	22	39

ultimate selective factor. Likewise, in the tropics, the proximate factors that initiate phenological changes may differ from the ultimate selective factors.

Physical cues that anticipate seasonality will vary with latitude within the tropics. At higher tropical latitudes, there is significant annual variation in photoperiod and temperature, and changes in both factors anticipate movements of the intertropical convergence zone and seasonal changes in rainfall, irradiance, and animal and microbial activity. Two examples will be used to illustrate the potential importance of photoperiod and temperature as proximate cues for tropical forest plant phenologies. The native range of the avocado (*Persea americana*) falls between 15° and 20° N, and reproductive buds differentiate in response to seasonal changes in temperature (Buttrose & Ambrose, 1978). The forest tree *Hildegardia barteri* occurs at 7° N, where photoperiod changes by 53 min, and a 1 hr decrease in photoperiod suppresses seedling leaf production (Njoku, 1963). Photoperiod and temperature cannot be uniformly important cues throughout the tropics; however, because photoperiod is constant at the equator, and seasonal temperature variation is negligible at the meteorological equator at about 5°N (Hastenrath, 1985), plants at these latitudes must respond to other proximate cues.

Rainfall and the restoration of plant water status after drought is the proximate cue for renewed growth in many deciduous and semideciduous forest plants (Opler, Frankie & Baker, 1976; Augspurger, 1982; Reich & Borchert, 1984). However, a large-scale forest irrigation experiment demonstrated that seasonal changes in soil moisture and drought were generally unimportant as phenological cues for canopy trees and lianas from semideciduous forest on Barro Colorado Island. Irrigation maintained soil moisture near field capacity for five consecutive dry seasons. Nonetheless, the timing of phenological events associated with the transition to the dry season (flowering and leaf fall) and also the transition to the wet season

(flowering) were unaffected in more than 95% of the species considered (Wright, 1991; Wright & Cornejo, 1990a,b). The absence of an effect of forest irrigation on tree and liana phenologies suggests that changes in atmospheric conditions that were not altered by irrigation may be important phenological cues.

A comparison of the timing of leaf fall from three sites in western Africa again implicates atmospheric conditions as an important phenological cue. Forests in the Ivory Coast, Nigeria, and Gabon experience two dry seasons (Hopkins, 1966; Bernhard-Reversat, Huttel & Lemee, 1972; Hladik, 1978). In the Ivory Coast and Nigeria, rainfall reaches its annual low from December through February. In Gabon, mean monthly rainfall exceeds 80 mm at this time, but falls to just 22 mm between June and August. If rainfall and soil drought were the proximate cue for leaf fall, then leaf fall would track rainfall, and the timing of peak leaf fall would differ between these three forests. In contrast, irradiance and potential evapotranspiration peak between December and February in all three forests. If atmospheric conditions were the proximate cue for leaf fall, then peak leaf fall would occur between December and February in all three forests, and this was, in fact, the case (Hopkins, 1966; Bernhard-Reversat, Huttel & Lemee, 1972; Hladik, 1978). In the low latitude tropics where variation in most physical factors is limited, changes in atmospheric conditions may become important cues for plant phenologies.

At least three possible mechanisms might allow atmospheric conditions to cue tropical forest plant phenologies. First, small temperature drops associated with heavy rainfall and with tropical incursions by cold air masses are both well established proximate cues for tropical forest plant phenologies (Wycherley, 1973; Ashton, Givnish & Appanah 1988). A second possibility is that seasonal increases in irradiance might cue production. A similar response is shown by many understory plants when production is initiated in response to increased irradiance shortly after the creation of a treefall gap. In this case, increased photosynthesis and increased tissue carbohydrate concentrations might trigger growth. The third possibility is that increases in potential evapotranspiration may create temporary water deficits that hasten the abscission of senescent leaves with limited control of transpiration (Reich & Borchert, 1984). This could trigger bud break, particularly in species where bud break is suppressed by the presence of old leaves (Borchert, 1983). Further studies of the mechanisms that control the timing of plant production in the low latitude tropics are clearly needed to explore these possibilities and identify other, as yet unanticipated, cues.

15.4 CONCLUSIONS

The timing of production by tropical forest plants can be predicted from seasonal patterns of rainfall and irradiance and mechanisms of drought resistance. Many more species produce leaves and reproduce in the season of greatest irradiance than expected by chance in evergreen forests and in seasonal forests, where peak irradiance occurs in the wet season. In seasonal forests where peak irradiance occurs in the dry season, disproportionately large numbers of species with adaptations that maintain dry-season water uptake produce leaves and reproduce in the drier, sunnier seasons, whereas species that lack these adaptations are limited to the wetter, cloudier season.

The strength of these community-level patterns and the universal effects of low light and water on plants suggest that these may be the primary evolutionary determinants of plant seasonality in tropical forests. Interacting organisms also create strong selective pressures on plant seasonality. For many tropical forest plants, these effects may fine-tune the timing of production within constraints imposed by the seasonal pattern of rainfall and irradiance.

The proximate mechanisms that control the phenologies of low-latitude tropical forest plants are largely unexplored. Evidence reviewed here suggests that atmospheric conditions, including cloud cover and atmospheric saturation deficits may be critical. Tropical deforestation increases atmospheric saturation deficits in surviving forest patches (Kapos, 1989) and on a larger scale, reduces evapotranspiration and convectional cloud cover (Salati et al., 1979). This raises the possibility that environmental conditions may change in tropical forest reserves as surrounding forest is removed (Shukla, Nobre & Sellers, 1990). These changes may disrupt the timing of plant production and alter interactions among species because very few reserves will be large enough to maintain the natural hydrological cycle. Tropical forests are being destroyed at a rapid pace. Global climate models indicate that deforestation will intensify seasonality in the tropics (Shukla, Nobre & Sellers, 1990). The possible consequences for forest plants in remnant reserves lends urgency to the study of tropical plant seasonality.

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