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THE PHENOLOGY OF TROPICAL FORESTS: Adaptive Significance and Consequences for Primary Consumers*

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Abstract

Most tropical woody plants produce new leaves and flowers in bursts rather than continuously, and most tropical forest communities display seasonal variation in the presence of new leaves, flowers, and fruits. This patterning suggests that phenological changes represent adaptations to either biotic or abiotic factors. Biotic factors may select for either a staggering or a clustering of the phenological activity of individual plant species. We review the evidence for several hypotheses. The idea that plant species can reduce predation by synchronizing their phenological activity has the best support. However, because biotic factors are often arbitrary with respect to the timing of these peaks, it is essential also to consider abiotic influences. A review of published studies demonstrates a major role for climate. Peaks in irradiance are accompanied by peaks in flushing and flowering except where water stress makes this impossible. Thus, in seasonally dry forests, many plants concentrate leafing and flowering around the start of the rainy season; they also tend to fruit at the same time, probably to minimize seedling mortality during the subsequent dry season. Phenological variation at the level of the forest community affects primary consumers who respond by dietary switching, seasonal breeding, changes in range use, or migration. During periods of scarcity, certain plant products, keystone resources, act as mainstays of the primary consumer community.

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INTRODUCTION

Inquiries into the phenology of tropical plants mostly take one of two approaches. The first is to examine the intrapopulational behavior of single species, or less commonly, groups of related species, in relation to environmental factors (6, 8). These studies focus on proximate physiological releasing mechanisms. While daylength, or daylength in combination with rising temperatures, often triggers the resumption of physiological activity after winter dormancy at higher latitudes (120), the limited annual variation in these factors in the tropics has prompted a search for other kinds of environmental signals that could serve as reliable indicators of season and/or as proximate releasers of physiological activity (6, 8, 109).

The second approach is to document the phenology of plant guilds or communities, in the interest of revealing broad, community-wide patterns of leafing, flowering, or fruiting (e.g. 31, 44, 46, 82, 83, 125). These studies are often used to generate indices to the food supply available to animal consumers. They only rarely address physiological mechanisms, but can offer insights into the ultimate evolutionary causes that may have selected for particular patterns of phenology.

It is conceptually important to distinguish between proximate factors that trigger a certain phenological event, and ultimate factors that have selected for a particular timing. Indeed, this distinction between proximate and ultimate causes originated in the study of plant phenology (10). Ultimate and proximate factors are usually different. For example, if the timing of a particular phenophase represents an adaptation to pressures exerted by animals, plants are likely to rely on changes in the abiotic environment to provide the trigger. Even if the phenological response is an adaptation to changes in abiotic conditions, ultimate factors and proximate triggers are not necessarily the same. For instance, many deciduous species of seasonally dry tropical forests drop their old leaves well before water stress has developed (165), and they produce new ones about one month before the onset of the rains (46, 60). By responding to a reliable environmental factor, a plant can initiate a developmental response in advance of a change in climate and so optimize phenological timing. Such discordance between particular physiological events and the more obvious landmarks of tropical climatic cycles has sewn confusion over the interpretation of proximate vs ultimate causes.

While our aim is to examine the ultimate factors influencing the timing of phenological events, all we can measure directly or manipulate experimentally are the relationships between phenology and proximate factors. Although experimental approaches are sometimes possible (2, 7), tests of adaptive hypotheses usually have to rely on comparisons, or on average or long-term

coincidences between phenological changes and the factor purported to serve as the selective force.

We first discuss whether phenological events can be considered adaptations. Next we attempt to evaluate the relative importance of biotic and abiotic selective pressures on the timing of phenological transitions in tropical woody plants. We see that both biotic and abiotic factors are involved in an interaction that defies a clear disentanglement of all variables. Finally, we consider the consequences of different phenological patterns for primary consumers. We do not conduct an exhaustive review of the literature, but rather attempt a synthesis of the available information on tropical phenology from which we draw some fresh conclusions.

The Phenophases and Their Interrelationships

The three phenophases (leafing, flowering, and fruiting) are not mutually independent in individual woody plants. Can hypotheses for their timing be considered for each phenophase separately, or should we instead consider any given phenological pattern as a single trait?

Fruiting must obviously follow flowering, and so questions about one might produce answers involving the other. Likewise, flowering and leafing can be interrelated. Axillary, ramiflorous, or cauliflorous flowering may be partly or wholly independent of leafing activity, but terminal flowering preempts the terminal buds of a plant and requires the initiation of a new set of shoots from lateral buds. Terminal flowering thus usually precedes leafing on the same branch. Many deciduous species show flowering and fruiting during the leafless phase (46, 70). In other deciduous species (19, 83, 103) and many evergreen ones (82, 109, 110), flushing and flowering occur on the same new shoots and therefore occur close in time. Very few studies have examined the possible functional significance of different interrelationships of the phenophases (or their link with tree architecture: 17). However, there is enough variability in their timing to suggest that the developmental programs of plants are flexible (44, 116, 125, 156). Hence, separate evaluation of evolutionary hypotheses for the timing of leaf emergence, flowers, and ripe fruits is warranted. However, whenever such flexibility is limited, we must expect plants to have evolved phenological patterns reflecting the external factor that exerted the strongest fitness effects.

Individuals and populations of tropical plants display nearly every possible phenological behavior from nearly continuous activity to repeated brief bursts, and from complete intraspecific synchrony to complete asynchrony (leafing: 46, flowering: 107, fruiting: 46, 98). Even in the most uniform tropical climates, however, only a tiny fraction of individuals shows continuous leafing, flowering, or fruiting (46, 50, 107, 110, 122, 151). Moreover, some

degree of intrapopulation synchrony is generally apparent, even though species vary from total independence, as in many figs (75, 86, 88, 151) and understory plants in everwet forests (161), to nearly absolute synchrony, as in many dipterocarps (6). Obligatorily outcrossing species, in particular, must show some synchrony in flowering (11, 13) and therefore in fruiting. Indeed, even at the community-level, seasonal rhythms are often apparent, not only in the seasonal tropics (46, 84) but even in equatorial regions (review in 125). This clumping in time and synchrony among individuals provides the basis for considering phenological events as adaptations to biotic or abiotic selective agents.

PHENOLOGY AS ADAPTATION TO BIOTIC PRESSURES

Because the impact of biotic factors on phenology has been thoroughly reviewed relatively recently (53, 120, 156), we consider their role here only briefly. The action of biotic factors may have led to either the minimization or the maximization of phenological overlap between plant species.

Staggering Phenologies in Time: The Competition Avoidance Hypothesis

Plant species may compete to attract pollinators or dispersers (46, 120, 136, 156) and thereby evolve behavior that minimizes phenological overlap with other plants dependent on the same animal vectors. Because plant-pollinator relations tend to be tighter than plant-disperser relations (50, 154), these conditions apply most readily to pollination. Moreover, related plant species may also benefit from divergent flowering periods in reduced production of interspecific hybrids of low fitness. Several examples of staggered flowering have been proposed (5, 6, 139, 156), but some of these have been challenged on statistical grounds (120). Similarly, some putative examples of staggered fruiting (24, 136) have proven to be indistinguishable from random sequences (116, 120).

Regardless of whether staggered phenologies may be rare or common, however, the communities from which staggered sequences have been described tend to be seasonal. The plants that compete most are members of the same pollination (or disperser) guilds and are often congeners. Thus, they are only subsets of their respective communities wherein multiple sets of internally staggered guilds may still merge to show clear community-level peaks (cf 116).

Clumping Phenologies in Time

Two kinds of biotic processes may lead to clumped phenologies. First, plants may time their activities in relation to the seasonally varying availability of

biotic agents. Second, they may attract pollinators and dispersers or satiate predators by doing so.

PRESENCE OF POLLINATORS OR DISPERSERS The seasonal presence or activity of animal vectors could select for temporally clumped phenological activity. Thus, the timing of the arrival of migratory birds may have selected for the timing of flowering of hummingbird-pollinated plants (34, 38), or bird-dispersed plants (9, 87, 89). However, it is difficult to distinguish these scenarios from the converse, that birds may time their migrations to coincide with phenology peaks (104). Moreover, in at least one site without migratory birds, the timing of fruit peaks was similar to that of climatically similar areas elsewhere (116).

Similarly, the abundance of pollinators may vary seasonally. For instance, it has been suggested that numbers of pollinating insects are highest during the dry season, favoring flowering at this time (44), but the reverse causality is equally likely (47, 117, 120).

ATTRACTING POLLINATORS A minimum flower abundance may be necessary to attract pollinators. Such a threshold may be attained through temporal synchrony (7), or through temporal synchrony and spatial clumping in combination, as exhibited by a number of low-density shrubs in a Costa Rican forest (84).

LOW ABUNDANCE OF HERBIVORES In the seasonal tropics, the abundance of insect herbivores may be lower during hot, dry seasons (73, 160). Moreover, herbivore damage is greatest on young leaves (29). Thus, plants producing new leaves during dry periods may experience reduced herbivory, a result obtained experimentally by Aide (2) for an understory shrub.

AVOIDANCE OF PREDATION Plants may swamp predators by producing vulnerable organs in concentrated bursts (7, 72). If different plant species share predator species, selection would favor interspecific synchrony of bursts, and so community-level peaks in phenological activity.

Leaves produced during flushing peaks sustain less damage than those produced out of synchrony (1, 2, 90). However, such a correlation is not always observed (27). In one study, chemically or mechanically protected plant species, which were subject to much less insect damage, did not show longer flushing periods (90). Studies are needed that can separate the effect of synchrony from that of timing per se (cf 2).

Species vulnerable to specialist (invertebrate) seed predators will not necessarily benefit from synchronizing reproduction, while those attacked by

generalist seed predators should show tighter synchrony in fruiting (65). Vulnerability to the latter increases with seed size (24). Species with large seeds tend to show a stricter clumping in time (24, 125, 134, 151), but exceptions are common (3, 50, 59).

Species or sets of species vulnerable to generalist seed predators may evolve highly clumped fruiting at supra-annual intervals (masting). In the temperate zone, masting is seen especially in trees with nonfleshy fruits, and it tends to be synchronous among species (15, 132). In the tropics, masting is documented in South American Lecythidaceae (125) and especially for the Dipterocarpaceae of the Malesian region (5, 74, 108). However, only in Malesia is masting a community-wide phenomenon (98, 151).

Masting, rather than strongly seasonal fruiting, may be due to two independent but non-exclusive processes. First, intermast intervals in Malesia are irregular and associated with El Niño Southern Oscillation events (74, 108), making it difficult for predators to entrain to the rhythm (6). Second, on nutrient-poor soils, crops produced during annual fruit peaks may not be large enough to swamp predators. It then becomes advantageous for plants to store carbohydrate reserves in a form inaccessible to predators and to produce larger crops at longer intervals (72).

Strong evidence for the hypothesis that masting is an adaptation to reduce seed predation comes from Silvertown's (132) comparative analysis in the temperate zone, showing that increased seed crop size is correlated with lower per capita seed predation risk, and that species subject to heavier seed predation in years of low fruit production are more prone to exhibit masting. For Malesia, the evidence is strong but less direct. First, among dipterocarps, fruiting is more synchronized between species than is flowering (5). Second, dipterocarp trees fruiting out of synchrony often lose all their seeds to predators (108, 157). Third, masting species tend to have large seeds that are only mechanically protected, whereas nonmasting species tend to have seeds that are small, endozoochorous, or wind-dispersed (74, 151), or are chemically protected (P Ashton, personal communication).

Relationship With Abiotic Processes

Phenological clumping in time can result from selection to attract pollinators, and/or to avoid seed predators or herbivores; such clumping leads to peaks separated by long periods with little or no activity. However, in such cases, the influence of biotic factors is arbitrary with respect to abiotic factors. Hence, whenever biotic processes favor phenological convergence, the strength of these processes may determine the sharpness of the peak, whereas climatic factors may determine its timing. It is therefore essential to consider the influences of climate on phenology.

PHENOLOGY AS ADAPTATION TO SEASONALITY IN ABIOTIC CONDITIONS

Tropical climates show predictable annual patterns. The intertropical convergence zone (ITCZ) of low atmospheric pressure, low wind speeds, and high rainfall follows predictably in the wake of the zenithal sun. Rainfall, sunshine, and temperature are thereby correlated in time, independent of the total annual rainfall. If passage of the ITCZ were to affect phenology, it would result in a predictable temporal relationship between phenology and latitude.

To test this possibility, we compiled the results of 53 phenological studies conducted in tropical forests around the world. For each study we recorded the month of peak phenological activity, using the maximum number of species, maximum number of individuals, or highest value of an ad hoc phenological index, as reported in the study. (These measures are highly correlated, and, where sample size is adequate, tend to peak closely together: 24, 30, 32, 44, 59, 125, 134, 146, 151).

The sun passes directly over all tropical localities twice a year. At the equator, the two occurrences correspond to the equinoxes. Toward the latitudinal limits of the tropics, the two occurrences fall closer and closer together in time, converging on the solstices. In Figure 1, the two lines represent the first of the two more proximate dates at which the sun passes directly over the localities indicated by the points. The results show clearly that community peaks of flushing and flowering closely track the march of the sun. Fruiting peaks, however, do not show any clear latitudinal pattern.

A large majority of the sites represented in Figure 1 conform to the general trend. The few exceptions fall into two categories. A small number of northern hemisphere sites show timing of flushing and flowering appropriate to the southern hemisphere. Most of these are slightly north of the equator in South America, where the so-called meteorological equator (defined with reference to air pressure; 137) falls between ca. 5° and 10° N. Sunshine and rainfall peaks are displaced accordingly (137). The remaining exceptional sites are in southeastern Brazil, where orographic effects of high coastal mountains generate an unusual timing of rainfall and sunshine in relation to the solstice (see 105). Apart from these few exceptions, the striking difference in timing between the hemispheres and the progression with latitude within each hemisphere demonstrate that tropical forests, like temperate ones, have a spring, even though they lack a a winter.

Hypotheses linking phenology to climate can be grouped into three broad classes. The first relates seasonal rhythms in plants to the presence of animals essential to completion of the reproductive process. We have already reviewed this hypothesis, for which the evidence is equivocal. Perhaps the best positive evidence was obtained by Foster (45), who showed that unseasonal rain in

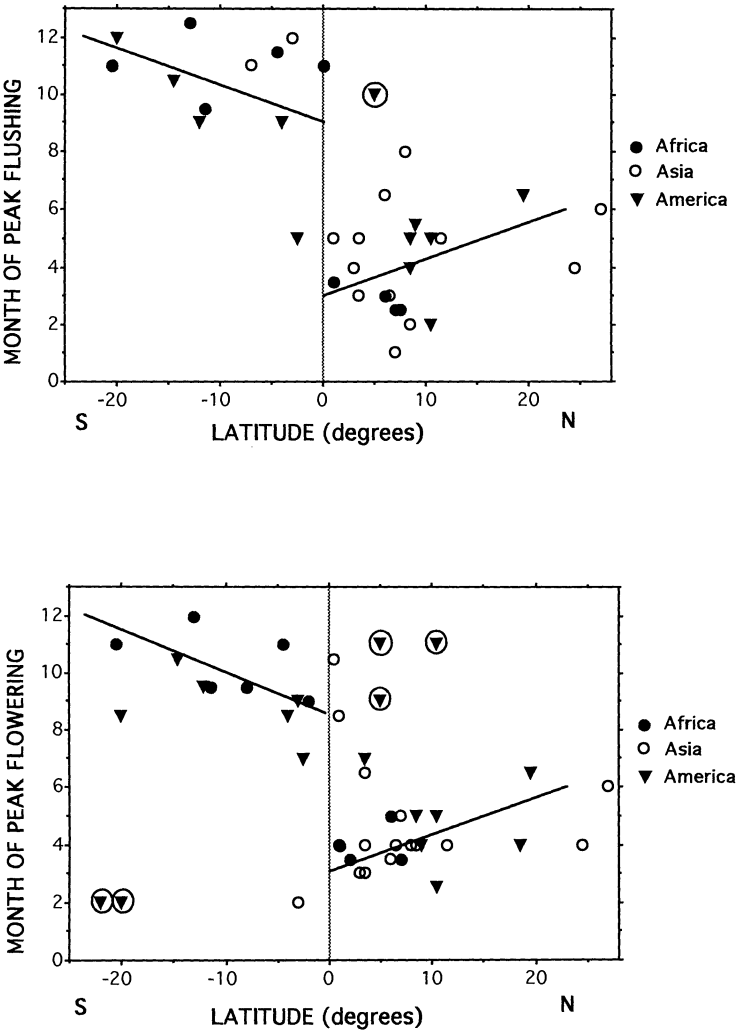

Figure 1 The months in which community-wide peaks in leafing (*a*) or flowering (*b*) are observed, in relation to latitude. The lines trace solar maxima as the sun moves toward higher latitudes. Phenological peaks clearly cluster around these lines. The data are culled from a total of 53 studies of tropical plant phenology (not all of which reported all three phenophases). Symbols surrounded by circles are discussed in the text. References and details can be obtained from the authors.

the dry season disrupted pollination and subsequent fruit set, presumably because it reduced the activity of pollinating agents. The second class of hypotheses argues that flowering or fruiting should take place in weather

conditions most conducive to pollination, dispersal, or germination. The third takes a physiological perspective, linking phenology to temporal variation in the levels of environmental factors that limit plant production. We now review the latter two classes of hypotheses.

Conditions Favoring Dispersal and Germination

WIND-DISPERSED SPECIES Some authors have argued that flowering and fruiting of wind-pollinated and wind-dispersed species should take place during characteristically windy parts of the year, especially when these coincide with periods of leaflessness (44, 70). Wind-pollination is rare in tropical plants (12, 13, 110), but wind-dispersal is relatively common, especially in deciduous forests and among lianas (54, 64). Several studies have confirmed that wind-dispersed species show peaks in fruiting at the windiest times of the year when canopies are bare (44, 46, 64).

However, if fruits dispersed by other means tend to peak at the same time, this would reduce the explanatory power of the hypothesis. The evidence is equivocal: although four studies did not show a clear difference in timing between the fruiting of wind-dispersed species and other wood plants (3, 50, 64, 125), two studies did (24, 44).

OPTIMAL TIME OF GERMINATION A second hypothesis argues that fruiting time is adjusted to precede the optimal moment for germination (46, 70, 117). This argument assumes that lying in a dormant state on the forest floor entails a significant respiratory cost or a high risk of seed mortality, or else that seedlings germinating at unfavorable times, e.g. late rather than early in the rainy season, experience higher rates of mortality (46). In accord with the latter expectation, germination in the seasonally dry forest of Barro Colorado Island shows a community-wide peak at the onset of rains (44, 49).

The optimal time of germination hypothesis predicts that more plants should time fruiting to coincide with the start of the rainy season in seasonally dry forests than in forests without a severe dry season. We can test this prediction using data from the 53 tropical sites. Dry months were defined as those with < 60 mm average rainfall (see 153). Nonseasonal sites were defined here as having no or one dry month per year, seasonally dry sites as having at least two dry months a year. The onset of the rainy season was defined as the first month with more than 60 mm of rain or, where no months were dry, as the month with the greatest increase in rainfall relative to the previous month.

Only 3 of 25 nonseasonal sites (12%) show community-level fruit peaks coinciding with the average month of "onset" of the rains or in the month preceding or following it, less than might be expected on the basis of chance (3-month period, hence 25%; Gadj. $= 4.94$, $P < 0.05$). In contrast, in

Table 1 Distribution of flowering-fruiting intervals of tropical forest sites (for which information on at least 20 species is available)

Site	Paleo/ Neotropics	Number dry months	Number species	Mean interval (months)	Coefficient Var.	% intervals >7 months	% intervals <3 months	source (Reference number)
Pasoh	P	0	86	4.48	45.2	5	24	110
Ketambe[1]	P	0	44	3.42	50.2	2	39	151
St. Elie	N	0	100	4.86	43.6	7	24	125
Alto Yunda	N	0	143	3.18	73.1	8	50	59
Barro Colorado[2]	N	3	71	3.69	65.2	6	39	44
Polonnaruwa	P	4	25	2.26	51.5	0	84	60a
La Pacifica	N	5	24	3.56	73.1	8	42	33
Chamela	N	6.5	94	3.46	66.7	6	57	19
Morondava	P	8	26	2.48	58.2	0	58	60

[1] excluding figs; [2] only trees

seasonally dry areas, 8 of 20 sites (40%) peak in these months. This is consistent with the prediction of the optimal time of germination hypothesis, though not significantly more than the expected 25%. However, the proportion of sites in seasonally dry forest with fruit peaks near the onset of the rains is significantly greater than in the everwet forest (Gadj. = 4.56, $P < 0.05$).

Flowering peaks in seasonally dry forests also tend to come at the end of the dry or at the start of the rainy season (33, 46, 70) and thus are very close to fruiting peaks. In Central America, there is a marked tendency toward bimodality in flower-fruit intervals, with many woody species showing very short intervals, but up to 15% showing intervals of close to a year (33, 44, 46, 127). Studies reporting flower-fruit intervals for more than 20 species are compiled in Table 1. There is some effect of the number of dry months on aspects of the flower-fruit interval distribution; the correlation with the percentage of species with intervals less than 3 months is significant (r_s = 0.73, $P < .05$). However, the effect of seasonal drought is confounded by a geographic effect.

The tendency toward bimodality of fruit maturation periods is stronger in the Neotropics than elsewhere, regardless of climate. Among those sites with data on flower-fruit intervals for more than 20 plant species, the percentage of species with intervals of 8 months or more is higher in the Neotropics than in the Paleotropics (Table 1; Mann-Whitney U test; $U = 0$, $P < 0.02$). Thus, a greater tendency toward a coincidence of the fruiting peak of the community with the onset of the rains should be apparent in Neotropical dry forests. In the comparative data set, this trend is also found but fails to reach significance, perhaps due to small sample size (31% of 13 Paleotropical sites vs 57% of 7 Neotropical sites).

Such intercontinental differences are even found among savanna trees: species in Côte d'Ivoire have a much longer period of fruit maturation than do species in Venezuela (128). The reasons for this geographic pattern remain obscure, but further research into dormancy and the attack of immature fruits by seed predators seems warranted.

Conditions Favoring Plant Production

Plant production is potentially limited by a small set of abiotic factors: water, sunlight, CO_2, and minerals. Significant seasonal variation in any of these factors could provide a selective force on phenological behavior. Plants may maximize production in a seasonal climate by avoiding the production of new leaves before or during unfavorable periods (e.g water stress), or by producing new leaves to coincide with the onset of periods of favorable conditions (e.g. high radiation). To develop more specific hypotheses, we briefly review tropical climates and consider seasonal variation in relevant abiotic factors.

SEASONALITY IN FACTORS LIMITING PLANT PRODUCTION Efforts to understand the effects of seasonality in tropical climates have focused almost entirely on patterns of rainfall. Consequently, seasonality in rainfall forms the basis for many classifications of tropical climates and vegetation (105, 153). In general, rainfall is high and aseasonal in a narrow band centered on the equator; it tends to peak twice a year a few degrees away from the equator, and once a year at greater latitude (thereby creating a single drought period of varied severity and duration). The typical latitudinal pattern can be significantly modified, however, by the proximity of mountain ranges or cold oceanic currents, and especially, by continentality (137). For instance, in maritime equatorial climates (e.g. parts of Borneo), there may be no seasonal drought, but areas with continental climates, notably central Africa and Amazonia can experience one or more dry months even on the equator.

Less obvious than seasonal variation in rainfall, and to date largely ignored by ecologists, is seasonality in solar radiation. As the solar zenith sweeps from hemisphere to hemisphere, the variation in incident intensity can be considerable. For example, when the sun is vertically above the Tropic of Cancer, the radiation falling on the Tropic of Capricorn is only 68% as great. Seasonally coupled with variation in solar radiation is cloudiness, which can greatly reduce the available radiant energy (91).

Seasonal variation in cloud cover, daylength, and solar elevation combine to generate substantial seasonal variation in irradiance. For sites in the wet tropics, total radiation averages 50% greater in the sunniest than in the cloudiest month (compiled from 105, 159). On Barro Colorado Island (at 9°N), the dry season peak in photosynthetic photon flux density is nearly twice that of the minimum in the wet season (159). In general, seasonality in cloud cover is most important near the equator, while other factors increase in importance toward higher latitudes.

Understory plants of tropical evergreen forests are severely light-limited (25–27, 113), but accumulating evidence indicates that even canopy trees may be light-limited (4, 130; D. Clark personal communication). Photosynthetic measurements show that canopy leaves generally operate below saturation (35, 111). Several lines of evidence point to the enhancement of photosynthetic and reproductive productivity by forest canopies during sunny periods. First, in everwet climates, productivity may peak in sunny, dry periods (92, 151). Second, dipterocarp masting is both more likely and heavier in years of high insolation (108, 151, 170). Third, cloudy conditions depress the productivity of several tropical crops, and high rainfall during fruit ripening may hamper ripening and reduce crop size (141). Finally, flowering is increased, flower-to-fruit intervals are reduced, and fruit weights are increased in sunny years (170). These observations suggest that phenological timing may be an adaptation to seasonality in irradiance.

HYPOTHESES AND TESTS We now examine the available information on the timing of phenological transitions for correlations with water, light, and nutrients.

1. *Water*. Correlations between tropical plant phenologies and rainfall seasonality abound. Drought is manifested in many seasonally dry areas by increasing deciduousness, diminished tree height, decreased leaf area index, and reduced vertical stratification, among other features (54, 96, 152, 157, 158). Conditions that plants experience as a drought can vary greatly, depending on temperature, humidity, and the availability of water in the soil, as well as intrinsic factors such as the extent and depth of the root system. Even modest water deficits impair growth and cell expansion, and plants under more severe water stress are unable to produce new organs (63, 150). For these reasons, it has frequently been inferred that water availability is both the proximate and ultimate factor controlling the phenologies of many tropical forest plants (121).

The water-limitation hypothesis can be tested by asking whether flushing and flowering peaks at the 53 sites coincide with the onset of the rainiest season for forests with > 2 dry months (mean monthly rainfall < 60 mm). The prediction is upheld. We found that the peaks of flushing and flowering fall within one month of the onset of the rainiest period in respectively 67% (Gadj. = 13.44, N = 18, P < .001) and 60% (Gadj. = 10.68, N = 20, P < .001) of strongly seasonal forests. In contrast, the comparable figures are just 33% and 33% for weakly seasonal forests (N = 18 and 24 sites, respectively).

Several mechanisms of drought resistance occur among tropical forest plants (37, 96, 106, 123, 127, 138, 167, 169). Reductions in leaf area, stomatal and cuticular conductance, and absorbed radiation all reduce transpirational water loss. Concurrently, deep roots, low resistance to xylem water flow, and high tissue osmotic potentials serve to maintain water uptake. As a consequence, evergreen and wet-season deciduous species that are adapted to grow and reproduce at the driest time of year occur in many of the driest tropical forests (37, 71). Many more species are able to maintain active growth during the dry season in less seasonal forests. On Barro Colorado Island, large-scale irrigation failed to influence the phenologies of most tree and liana species (165, 166).

2. *Insolation*. Young leaves that have just finished expanding are most efficient at photosynthesis (39) and at controlling transpirational water loss (99). They also have maximum effective leaf area, undiminished by accumulating herbivory, epiphylls, or pathological damage. Hence, in the absence of water limitation, it could be predicted that tropical plants should produce crops of young leaves to coincide with periods of high assimilation potential (cf 93, 151), i.e. high insolation.

The prediction can also be extended to flowering on the ground that it is energetically most efficient to transfer assimilates directly into growing organs rather than store them for later translocation (22). Thus, we can also predict that flowering coincides with periods of peak insolation in everwet areas, and more generally, that the emergence of young leaves and the onset of flowering should be closely related in time. Such a close relationship has often been observed within species (see above) and is also apparent at the community level. In the 32 tropical sites for which both flushing and flowering information was available, 10 (31%) showed peaks in the same month, and 19 (59%) showed peaks differing by one month in either direction. No corresponding prediction can be posited for the timing of fruit ripening, which depends mainly on the life history tactics of the particular species.

The insolation-limitation hypothesis has been tested at the species level (168). Twice as many species as expected centered their leafing and flowering around the sunniest trimester of the year in three different Neotropical everwet forests. In four different seasonally dry forests, all species with shallow root systems (unlikely to maintain water status during the dry season) concentrated leaf production in the wetter season, while two thirds of the deep-rooting species flushed and flowered in the sunny (dry) season. Observations by Opler et al (112) also support this idea. In a dry forest, treelets and shrubs of the uplands concentrated leaf production at the start of the rains, but those near the river peaked just before the start of the dry season. Thus, tropical trees tend to concentrate flushing and flowering during the sunniest time of the year, except when prevented from doing so by water stress.

We can also test this hypothesis with community-level data from the 53 sites mentioned above. In the absence of data on photosynthetically active radiation for most sites, we substituted information on the monthly duration of sunshine from the original or other studies at the same site, or from general climate reference works (18, 58, 105, 131). In everwet areas, 53% of the flushing peaks ($n = 17$) fell within one month of the month of maximum duration of sunshine, about twice the number expected by chance (Gadj. = 5.88, $P < 0.05$). This effect is weaker in seasonally dry forests (33%, $n = 18$; n.s.), in which flushing tends to peak about two months later. As to flowering, 39% of the community-wide peaks are associated with the month of highest sunshine in everwet forests (n.s.), vs 50% (twice the expected value) in seasonally dry forests ($n = 20$; Gadj. = 5.61, $P < 0.05$). Thus, community-level patterns also support the hypothesis, given that duration of sunshine roughly approximates total radiation.

Cloud cover reduces direct beam radiation more than diffuse radiation (36). Seasonal variation in cloud cover can thus result in differential effects among forest strata. The understory of deciduous forests experiences wide extremes of seasonal variation in irradiation (36, 80). In contrast, the understory of

everwet forests, relative to the canopy, receives a far greater proportion of photosynthetically active radiation in the form of diffuse light (14). Thus, in these forests, the understory may experience less seasonality in irradiation, and thus in phenology, than the canopy. Several studies confirm this prediction (84, 112, 125, 161); in all of them, the weak peak in understory flushing or flowering coincides with the sunnier parts of the year.

3. *Nutrient uptake or loss.* Vegetative activity may be timed to maximize uptake of a seasonal nutrient pulse released by decomposing leaf litter after the start of the rainy season. Nutrient uptake requires active transpiration, so plants could maximize transpiration by producing young leaves as the rains begin. This hypothesis cannot easily be distinguished from the water stress hypothesis, which is likely to be the more general one. Moreover, trees can store and internally recycle nutrients (21), and the importance of seasonality in nutrient availability in tropical forests is unclear. In low fertility environments, nutrient loss is minimized through increased leaf retention times (76, 127).

Conclusion

The phenology of tropical woody plants has been shaped by both biotic and abiotic selective factors. This review demonstrates a major role for abiotic factors, in particular irradiance and water stress. Biotic factors are frequently less pervasive and may affect only species or guilds of species. Where they affect the community, the selection is often for synchrony rather than any particular timing.

Beyond these emerging generalizations, we must keep in mind that plants must cope with numerous external biotic and abiotic factors that impinge on their fitness, each of which may select for particular phenological responses. In some cases, the pressures exerted by independent selective factors tend to coincide. For example, by flushing and flowering during periods of high illumination, plants may improve herbivore avoidance, pollination success, and net photosynthesis. However, the pressures of external factors can also select for incompatible outcomes. The challenge now is to design phenological studies to examine how plants integrate the action of numerous, sometimes conflicting, abiotic and biotic factors.

ANIMAL ADAPTATIONS TO TEMPORAL VARIATION IN RESOURCE ABUNDANCE

One generalization to emerge from community-level phenological studies is that plant production of consumer resources (fruit, seeds, flowers, flush leaves) undergoes temporal variation in virtually all tropical forests (125), especially those in seasonal environments (46, 84). Both within-year and

between-year variation in resource production can be pronounced, but multi-year records are as yet available for only a few sites. Periodic and, especially, prolonged resource scarcity has presumably led to the evolution of a wide range of morphological, behavioral, and physiological adaptations in primary and even secondary consumers (145). These adaptations confer the flexibility needed to survive in environments characterized by fluctuating or unpredictable food supplies.

A second generalization is that during periods of resource scarcity, certain plant products, dubbed "keystone plant resources," assume major importance as mainstays of the primary consumer community (58, 61, 62, 147, 148).

The abundance of these resources may set the carrying capacity of the consumer community, while the physical and nutritional properties of keystone resources appear to determine some morphological features of consumer species. Empirical evidence bearing on these two points are reviewed below.

Adaptations to Scarcity

OCCASIONAL FAMINE AND MASS MORTALITY Scanty evidence suggests that food scarcity only rarely becomes severe enough for long enough to result in mass starvation of vertebrate consumers. The best documented cases are from Barro Colorado Island. Foster (45) records 4 episodes of extreme famine, and 10 episodes of mild famine in a 51-year period, all associated with anomalously heavy rains in the later part of the dry season. Unseasonal rains resulted in the subsequent failure of many species to fruit in the ensuing wet season. More generally, howler monkeys and coati mundis died on Barro Colorado Island in greater than usual numbers during the normal period of fruit scarcity in the latter part of the rainy season (79, 102). Apart from Barro Colorado Island, which no longer holds jaguars, pumas, and harpy eagles, and which is noted for high mammal densities (56, 67), evidence of animal starvation in more humid tropical forests is lacking. In 18 years of observations at Cocha Cashu, Peru, and in 16 years of observations at the Ketambe, Sumatra, we have not found evidence of mass mortality of primates or other mammals. Possibly, in these forests, many primary consumers may be kept at sufficiently low population densities by predators that death by starvation is rare.

SEASONAL FOOD SCARCITY AND DIETARY SWITCHING Less dramatic indications of dietary stress are routinely observed during seasonal periods of scarcity: seasonal weight loss in marsupials and primates (24, 57), increased trappability of terrestrial mammals (133), and retarded growth rates of juvenile rodents (133). During periods of scarcity, many mammals (less often, birds) resort to feeding on materials that (i) are of low nutritional value (e.g. bamboo,

pith, fleshy petioles, twigs—16, 146; nectar—68, 114, 129, 144, 149), (ii) are protected by hard coverings, which increase handling time (e. g. palm nuts—66, 69, 140, 146), (iii) contain chemical deterrents, which limit the quantities that can be ingested (mature foliage—52, 95, 101; immature fruits—43, 146), or (iv) are diffusely distributed in the environment, so that more time must be invested in searching (e.g. nectar, insects, 146).

Of all the behaviors that serve to mitigate the impact of scarcity, dietary switching appears to be the most important. Within the guild of frugivorous primates at Cocha Cashu, Peru, for example, species alter their diets as follows: tamarins and night monkeys turn to feeding on nectar (144 and 164); spider, howler, and titi monkeys eat more leaves (101, 142, 164); squirrel monkeys engage in day-long insect foraging bouts (146); and capuchins bite open hard palm nuts (146).

The opportunities for dietary switching of this kind are closely tied to phenological patterns, depending, for example, on whether two categories of resources vary in concert or in opposition over the seasonal cycle. Accordingly, the biomass of primate communities tends to be low where peak abundances of fruit and foliage occur simultaneously, as in the neotropics, because seasonal switching is precluded, and high where the periods of peak abundance are seasonally offset, as in central Africa (145).

SEASONAL BREEDING The reproductive cycles of many birds and mammals show regular seasonal rhythms, even near the equator (42, 85, 100, 135, 161). Frequently the energetic costs of reproduction (lactation or provisioning of fledglings) reach maximum levels during the period of greatest abundance of food (20, 57, 124). Statistically verified aseasonality of reproductive activity has been noted most frequently in mammals that have long gestation and rearing periods, which make impossible the avoidance of energetic stress at some point in the period of dependency (81).

SEASONAL MOVEMENTS Tropical animals often expand their home ranges, or shift their use of habitats in a seasonally predictable fashion. Such shifts can occur on a wide range of spatial scales. Animals may move around within a local habitat mosaic according to a regular seasonal pattern: birds (77, 78, 88, 155, 162), insects (73), primates (67, 115, 146), forest ungulates (16, 80), fruit bats (41). At Cocha Cashu, Peru, such local movements correspond with seasonally staggered fruiting peaks in a series of habitats (67). Occasionally, consumers may take the opposite tack and reduce the daily foraging path or area searched during times of food stress (28, 146). Such behavior can be interpreted as an energy conserving measure when greater exertion does not yield commensurate gains in food intake.

NOMADIC BEHAVIOR Nomadism in tropical forest vertebrates is not well documented, although anecdotal accounts implicate a variety of nectivorous, frugivorous, and granivorous birds (97), as well as certain mammals, notably, bearded pigs in Asia, mandrills and elephants in Africa, and white-lipped peccaries in the Neotropics (80). Nomadism may be more prevalent in bats than is currently realized.

ALTITUDINAL MIGRATION Movements up and down mountain slopes have been investigated with radio-tagged birds. Of the species showing altitudinal movements, nearly all are highly dependent on plant resources, especially nectar and fruits (94, 126, 143, 155). Altitudinal migration of avian frugivores appears to be less frequent in New Guinea, where only one of eight species of radio-tagged birds-of-paradise showed a statistically significant seasonal displacement of its altitudinal range (118).

Seasonal altitudinal movements may be a response to temporal shifts in fruiting peaks with altitude, at least in Sumatra (C. van Schaik & Djojosudharmo, unpublished), and in Malaysia (30, 91, 119; see also 163).

HIGH-TEMPERATURE HIBERNATION In the most dramatic adaptation to food scarcity, certain tropical insectivores and frugivorous vertebrates (Malagasy tenrecs and cheirogaleid prosimians) hibernate for as much as six months, notwithstanding ambient temperatures up to 30° (23).

Keystone Plant Resources

In many tropical forests there seem to be a few plants that regularly produce edible reproductive structures (fruits, seeds, or flowers) during the annual period of minimum fruit availability. The products of these plants have been termed "keystone plant resources" (147, 148). In the floodplain forest at Cocha Cashu, Peru, for example, only a dozen species of plants (including trees, stranglers, vines, and palms), in a total flora of over 1000 species, produce such keystone resources (146, 147). Distinguishing keystone species from others that may flower or fruit only sporadically during the time of general scarcity, or that may produce fruits that are little used by the animal community, requires a thorough knowledge of both the local flora and the dietary habits of the principal vertebrate consumers. It should be noted that a given animal species may rely on totally different keystone resources in different habitats or regions (compare 147 with 48 or 114).

A sufficiently comprehensive overview of plant-vertebrate interactions has been assembled for only a few tropical sites (Kutai, Indonesia—88; Cocha Cashu, Peru—147; M'Passa, Gabon—51). Fragmentary information is available for Barron Colorado Island (55, 62, 133, 134). Although it is risky to generalize from so small a sample, strangler figs are prominent among the

keystone plant resources at the Neotropical and Asian sites (see also 86). However, figs do not play such a role at M'Passa (51), nor at certain Amazonian terra firme sites (114). Further studies are obviously needed before broader patterns emerge.

CONCLUSION

Despite early speculation to the contrary, all tropical forests studied to date show pronounced phenological variation between seasons and/or between years, creating a boom and bust environment for consumers. The frequency, severity, and duration of scarcity vary greatly from forest to forest, and the corresponding impacts on consumer communities are likely to vary accordingly. Adaptations to scarcity include dietary switching, seasonal breeding, seasonal increases or decreases in ranging, migration, and even (rarely) hibernation. Impacts of seasonal rhythms in food supply on the structure and biomass of consumer communities are just beginning to be explored (40, 145).

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