

Phenology and Stem Diameter Increment Seasonality in a Costa Rican Wet Tropical Forest

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ABSTRACT

The relationship between phenology and tree stem diameter increment is largely unexplored in tropical species, especially in wet tropical forests. To explore links between these phenomena, we measured stem diameter increment and phenology of ten canopy tree species from a range of functional types in the Atlantic lowlands of Costa Rica to test for seasonal and interannual patterns. We measured stem diameter increment using band dendrometers and visually assessed leaf and reproductive phenology monthly from 1997 to 2000. We categorized the species into groups based on patterns of leaf exchange and reproduction. Species were either deciduous with synchronous or asynchronous leaf drop, or evergreen with continuous or seasonal leaf flushing. Flowering occurred supra-annually, annually, or continuously. Of the ten species studied, four species, *Cecropia insignis*, *Dipteryx panamensis*, *Lecythis ampla*, and *Simarouba amara*, had consistent seasonal stem diameter increment patterns in both years. *Dipteryx panamensis* and *L. ampla* were deciduous with synchronized leaf drop. *Cecropia insignis* was evergreen and produced new leaves continuously. *Simarouba amara*, also evergreen, exchanged leaves over a brief period once a year. We tested whether stem diameter increment was correlated to phenology using logistic regression. Leaflessness significantly explained patterns in stem diameter increment but reproductive phenology did not. Deciduous trees were 2.6–9.3 times more likely to grow less than average the month following leaf fall than in months when trees had full crowns.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: La Selva; tropical rain forest; tropical tree stem diameter increment.

SEASONAL STEM DIAMETER INCREMENT AND LEAF TURNOVER are well-known phenomena of temperate and seasonally dry forests. Rhythmic stem diameter increment and phenological responses also occur in less-seasonal biomes such as wet tropical forests, although these responses can be subtle or infrequent in comparison. The proportion of species with synchronized phenology in tropical forests is proportional to the strength of environmental cues, primarily rainfall. Seasonally dry forests are often dominated by seasonally deciduous species, whereas in continually moist forests, deciduous species become less common (Frankie *et al.* 1974, Medina 1983, Kikuzawa 1991, Reich 1995). Annual rhythms of leaf turnover and stem diameter increment exist even in very constant environments, and seasonal cues in the wet tropics have been shown to affect annual stem diameter increment response patterns in some species (Hazlett 1987, Breitsprecher & Bethel 1990, Newstrom *et al.* 1994, Corlett & LaFrankie 1998, Worbes 1999, Fichtler *et al.* 2003, Borchert *et al.* 2005) though not in all (Wright & Cornejo 1990).

Stem diameter increment and phenological events can be controlled by endogenous or exogenous factors. The degree of synchrony in phenological responses can indicate the control source: asynchronous responses are likely governed endogenously, whereas concerted responses are initiated by climatic, light, or other external

stimuli such as floods (Borchert 1983, Ashton *et al.* 1988, Schöngart *et al.* 2002). Endogenous responses can be secondarily entrained by environmental cues (Borchert 1992). Light and rainfall are most often identified as the climatic factors driving phenological seasonality in the tropics though other species in weakly seasonal environments might not respond at all to small annual variations of light and rainfall (Ashton *et al.* 1988, Wright & van Shaik 1994, Bullock 1997, Borchert 1998, Borchert & Rivera 2001).

The effects of phenology on stem diameter increment are not well understood in weakly seasonal forests. Although a few studies have examined the seasonality of tree bole stem diameter increment and the inferred climatic causes in the tropics (Hazlett 1987, Breitsprecher & Bethel 1990, Bullock 1997), the link between tropical tree phenology and stem diameter increment in wet forests has not been explicitly explored. In this paper, we describe patterns of leaf turnover and reproductive phenology as well as explore the relationship between these phenological events and canopy tree stem diameter increment among species with a diversity of life histories and phenological traits.

METHODS

STUDY SITE.—The study site was a stand of old-growth forest at La Selva Biological Station, Costa Rica (10°26' N, 83°59' W). The climate and site description of La Selva are detailed in McDade *et al.*

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(1994). Climate measurements reported here were collected at an on-site weather station maintained by the Organization for Tropical Studies. Rainfall is heavy throughout the year, with two drier periods: February through April, and during September. Average daily rainfall decreases by approximately half during the peak drier period when compared to the wettest months. Nevertheless, even in March, the driest month, the average 158 mm of rain, according to Walter (1985), indicates a moisture surplus. In comparison, on Barro Colorado Island in Panama, a tropical forest that shares many tree species with La Selva, rainfall in March, the driest month, averaged 23 mm during 1972–1989 (Leigh 1999). The lowest soil moisture recorded in the study occurred in April of 1998 and averaged $0.50 \text{ m}^3/\text{m}^3$ which was unlikely to produce severe moisture stress.

Day length at La Selva varies slightly annually, with about 1.23 h more daylight in June than in January (Forsythe *et al.* 1995). Irradiance levels at La Selva are less affected by astronomically driven changes in day length than by declines in direct irradiance caused by seasonal differences in cloud cover (Graham *et al.* 2003). Yearly temperature variation at La Selva is also relatively small; differences in the average daily maximum and minimum temperatures of the warmest and coldest months are $< 3^\circ\text{C}$. Daily temperature variation is usually $< 10^\circ\text{C}$; in 1999, the average daily maximum air temperature was 29.7°C , and the average daily minimum was 22°C . Though subtle, the seasonal variation at La Selva is sufficient to provide cues for synchronized phenological events such as flowering and leaf turnover in many tree species (Frankie *et al.* 1974).

STUDY SPECIES.—The ten species we chose for this study are a diverse group of canopy and emergent trees, with a range of life-history, anatomical, and morphological traits and have had long-term annual stem increment measurements (Table S1). These species also comprise a significant portion of the biomass of the forest; *Pentaclethra macroloba* alone makes up 40 percent of the timber volume at La Selva (King 1996). Clark and Clark (1992, 1999) categorized nine of the ten species into four functional groups based on patterns of establishment and regeneration and five groups based on annual stem diameter increment across sizes classes. We randomly chose individuals from a subset of trees studied by Clark and Clark (1992) with the addition of ten randomly chosen individuals of *P. macroloba*, a forest dominant. Selected trees had to meet the following criteria: a diameter of 30–60 cm above buttress and unobstructed or emergent crowns. Trees in this size class have the highest stem diameter increment rates, with the exception of *Cecropia obtusifolia*, which had higher stem diameter increment rates in smaller size classes (Clark & Clark 1999).

STEM DIAMETER INCREMENT MEASUREMENTS.—Initially, we installed 115 steel band dendrometers (Liming 1957) on ten or more individuals of the ten study species between January and July 97. Mortality and band damage reduced the final sample size of trees with measurements spanning the full study period to seven to ten individuals (Table S1). The bands were read once a month from the time of installation until March 2000. We used a micrometer caliper to measure the distance between a fixed mark on the band and the

dendrometer sleeve, and recorded the distance to the nearest 0.01 mm. For this study, we report the results from trees that grew more than 2 mm in diameter over the entire 2-yr measurement period. In May 1999, we installed a second band on three of the already banded individuals of each of the ten species to determine the time required for the bands to settle and give consistent readings. Usually, slack remaining in the bands after installation introduces measurement error that is reduced through time as stem growth removes the slack (Keeland & Sharitz 1993). We read these additional bands simultaneously with the original bands. The data from duplicate band installation indicated that stem diameter increment readings were not significantly different after 1 mo.

While a repeated measures ANOVA indicated that there was a significant within-subjects effect ($F_{5,28} = 4.61$, $P = 0.003$), there were no differences ($P > 0.05$) among any combination of within- and between-subject effects, indicating that there were no differences between the band readings. The lack of discrepancies between the early band readings apparently was due to careful tightening of the bands upon installation and a rapid increase in stem diameter that quickly removed any residual slack.

PHENOLOGY.—We assessed leaf and reproductive phenology when the bands were read. Using binoculars, we visually estimated the proportion of the crown occupied by four classes of leaves and reproductive structures: mature dark green leaves, young (red or light green) or unexpanded leaves, and flowers and fruit. Visual estimates with binoculars have been successfully used in several phenological surveys in the tropics (*e.g.*, Kimura *et al.* 2001, Laurence *et al.* 2003). Errors associated with visual cover estimates have shown that individual observations are consistent, but can be biased (Sykes *et al.* 1983). To minimize error variance due to observer, the same person made all the phenological observations. Furthermore, we established broad indices that would facilitate a rapid and more accurate classification of the crown status. For each phenological category, the observer assigned an index from 0 to 3 based on the percentage of the full crown potential occupied by each category. The observer scored a 0 for a bare crown, a 1 for 0–25 percent, 2 for 25–50 percent, and a 3 for > 50 percent cover of the crown occupied by each class. We did not visually assess the phenology of *P. macroloba* due to its dense canopy. For the *Cecropia* species, the observer could not differentiate between flowers and fruit so phenology scores reflected the presence or absence of reproductive structures.

DATA ANALYSIS.—We first explored whether tree stem diameter increment had a seasonal rhythm. A plot of tree stem diameter increment with time as the x-axis shows a waveform if stem diameter increment is seasonal and synchronized. Analyzing the stem diameter increment as a wave allowed the identification of the period as well as the season of maximum and minimum stem diameter increment. We used Fourier analysis to objectively test for periodicity in stem diameter increment. To correct for differences in the day of the month sampled, we linearly interpolated adjacent sampling values to the diameter on the 19th of each month as the dependent variable. We chose the 19th to maximize the time period with

continuous records. Stem diameter increment rates can vary considerably among individuals based on local conditions. Since this variance could mask seasonal rhythms, we used standard increment scores for the Fourier analysis. These were calculated by subtracting the mean increment from each observation and divided this value by the increment standard deviation. This was done on a tree by tree basis, and then averaged by species. This also had the added benefit of removing the autocorrelated trend in cumulative stem diameter increment among sequential observations that could also mask seasonal rhythms. We tested the relationship between phenology and stem diameter increment using logistic regression. The independent variable was crown phenological index and the dependent was a score of whether the current month's stem diameter increment was greater or less than the previous month's stem diameter increment.

RESULTS

PATTERNS OF PHENOLOGY.—The ten species fell into two main leaf phenological categories: those with evergreen or deciduous crowns. Two subcategories were further differentiated by timing of leaf turnover occurred within each main category (Table 1). We also categorized the species into three reproductive groups (Table 1). The four deciduous species were leafless at least once a year: *Balizia elegans*, *Dipteryx panamensis*, *Hymenolobium mesoamericanum*, and *Lecythis ampla* (Table 1). Individuals of these species were generally leafless for a month or less and species differed in leaf shedding synchrony: *D. panamensis* and *L. ampla* individuals tended to drop leaves in concert (Pearson $\chi^2 = 22.2$, $P = 0.023$; $\chi^2 = 42.7$, $P < 0.0001$, respectively), whereas individuals of *B. elegans* and *H. mesoamericanum* dropped leaves independently of each other (Pearson $\chi^2 = 12.6$, $P = 0.32$; $\chi^2 = 16.4$, $P = 0.13$, respectively) (Fig. S1). Only *H. mesoamericanum* trees shed all their leaves more than once a year and an individual tree could be leafless at almost any time of year. *Dipteryx panamensis* and *L. ampla* trees lost leaves during the driest months from February to May. Most, but not all, of *B. elegans* trees flushed new leaves from June to September. The degree of synchrony in leaf shedding of *B. elegans* was intermediate between that of *H. mesoamericanum* and *D. panamensis*.

One evergreen species, *Simarouba amara*, flushed more new leaves from January to April when light levels were highest and rainfall lowest (Fig. 1). While flushes of new branch growth in the evergreen species could be mistaken for leaf turnover, in *S. amara*, the majority of the canopy was observed to be occupied by new, incompletely expanded leaves. The remaining species, *Miconia guianensis*, *P. maculosa*, *Hyeronima alchorneoides*, *Cecropia insignis*, and *C. obtusifolia*, seemed to flush leaves continuously (Table 1).

The ten species flowered in three general patterns: supra-annual, continual, and annual (Newstrom *et al.* 1994). Species with annual flowering patterns tended to flower at particular times of year (Fig. 2). The timing of flowering in *C. insignis*, *D. panamensis*, *L. ampla*, and *S. amara* occurred immediately following the months with highest light and lowest rainfall. Two taxa, *H. mesoamericanum* and *M. guianensis*, flowered supra-annually, though the degree of flower production differed. *Hymenolobium mesoamericanum* had a mast flowering event just prior to the beginning of our measurements. *Miconia guianensis* only flowered sporadically during the observation period and never produced flowers in abundance. Only *C. obtusifolia* produced reproductive structures continuously. Few *B. elegans* and *H. alchorneoides* individuals we followed flowered; therefore we did not find any seasonal phenological patterns in these species.

There was no broad correlation between the timing of leaf turnover and timing of flowering: *e.g.*, *H. mesoamericanum* had annual leaf turnover but flowered supra-annually and *S. amara* had no annual leaf turnover but flowered annually. The timing of leaf and reproductive phenology was linked in two species; *L. ampla* and *D. panamensis* both flowered shortly after leaf turnover.

STEM DIAMETER INCREMENT.—Plots of the monthly stem diameter increments showed that two deciduous species, *D. panamensis* and *L. ampla*, had rhythmic stem diameter increment (Fig. S2). The slowing of stem diameter increment seemed to coincide with the periods when these species were leafless. Two evergreen species, *C. insignis* and *S. amara*, also appeared to have seasonal stem diameter increment (Fig. S3). The stem diameter increment trajectories of the remaining evergreen and deciduous species did not appear to fluctuate regularly or have seasonal rhythms. These patterns were

TABLE 1. Phenological groups of the ten tree species in Costa Rica.

Species	Phenological functional group	Timing of new leaf production	Synchrony of leaf turnover	Flowering
<i>B. elegans</i>	Deciduous	Annual	Asynchronous	Annual
<i>D. panamensis</i>	Deciduous	Annual	Synchronous	Annual
<i>L. ampla</i>	Deciduous	Annual	Synchronous	Annual
<i>H. mesoamericanum</i>	Deciduous	Sub-annual	Asynchronous	Supra-annual
<i>C. insignis</i>	Evergreen	Continuous		Annual
<i>C. obtusifolia</i>	Evergreen	Continuous		Continual
<i>M. guianensis</i>	Evergreen	Continuous		Supra-annual
<i>P. maculosa</i>	Evergreen	No data		No data
<i>H. alchorneoides</i>	Evergreen	Continuous		Annual
<i>S. amara</i>	Evergreen	Annual	Synchronous	Annual

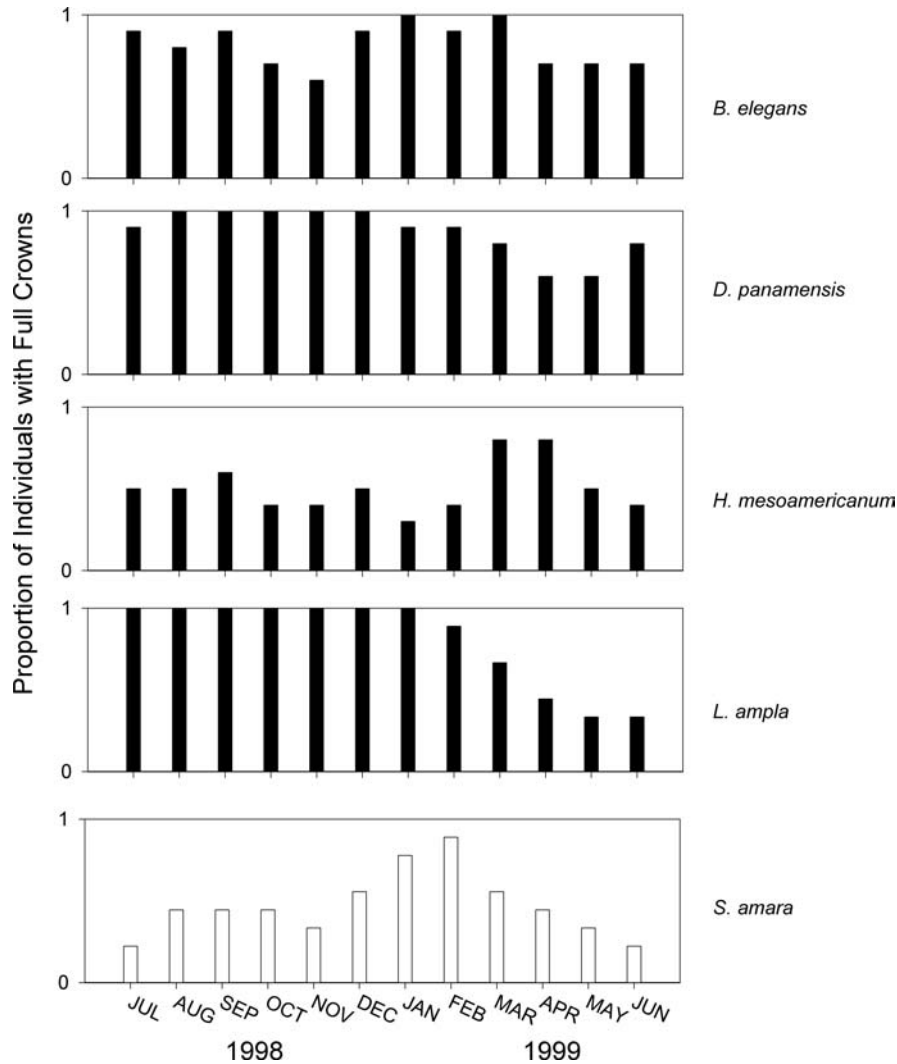


FIGURE 1. Seasonal leaf cover for species showing seasonal patterns of leaf drop or flushing. The proportion of individuals of deciduous species with canopies occupied by < 75 percent leaf cover of mature leaves (solid bars) or evergreen species with 25 percent or more cover of newly expanded leaves (open bars).

verified by the Fourier analysis results. In the four cases where there was a significant rhythm, stem diameter increment maxima occurred in September and minima in March ($P < 0.05$). A repeated measures ANOVA showed a significant three-way interaction among species, month, and year (Pillai's Trace = 1.71, $P < 0.001$). Mean monthly stem diameter increment rates ranged from 0.21 mm to 0.88 mm. Although yearly mean stem diameter increment varied among some combinations of species, it did not vary within species and was not grouped by any particular phenological traits (Fig. 3).

EFFECTS OF PHENOLOGY ON STEM DIAMETER INCREMENT.—Logistic regression analysis of the effect of leaflessness on stem diameter increment showed that stem diameter increment in months following leaf shedding was significantly slower than in other months in all the deciduous species except *B. elegans* (Table 2). Other lags did not show as strong an effect. Trees without a full canopy of leaves the month before measurement were 2.6 (*H. mesoamericanum*), 4.4 (*L.*

ampla), and 9.3 (*D. panamensis*) times more likely to grow less than average than trees with a full crown. *Balizia elegans* trees without leaves were less likely to grow as well as fully leaved trees, but the effect was not significant at $\alpha = 0.05$, which was due to the small number of leafless trees during the study period. For evergreen trees, we tested the impact of leaf flushing on stem diameter increment and found no relationship ($P > 0.05$). We applied comparable tests on the relationship between reproductive activity and stem diameter increment. We found no significant effect of reproduction on stem diameter increment for any species (all $P > 0.05$).

DISCUSSION

Our results indicate that an array of life-history traits was correlated with rhythmic stem increment and/or phenology in several species even in this very wet, nearly aseasonal climate. Even so, seasonal

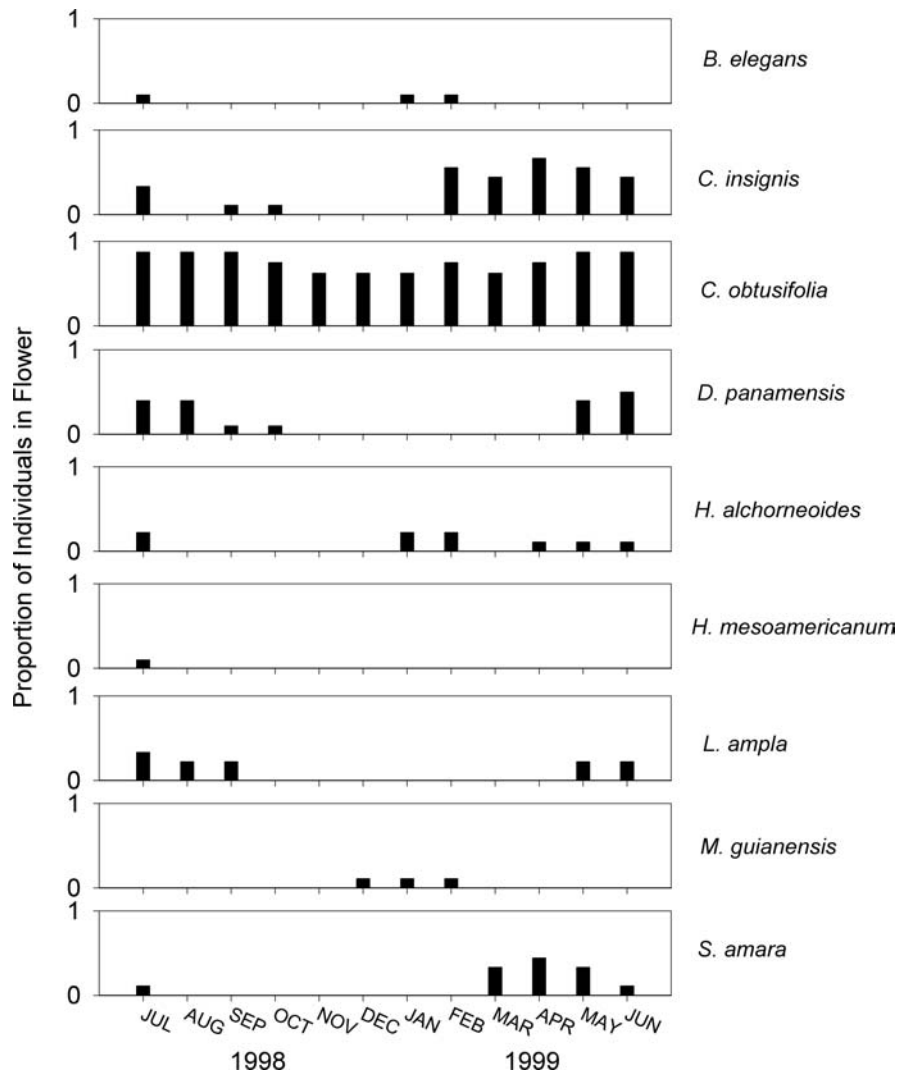


FIGURE 2. Flowering phenology of the study species. The bars represent the proportion of the trees flowering at least 25 percent capacity (inferred from crown size).

pulses in leaf or reproductive phenology did not always result in a detectable effect on stem increment measurements. The most consistent patterns that emerged from our analyses were that periodic deciduousness or a pulse of canopy leaf turnover was the most important predictor of seasonal variation in stem diameter increment. Not surprisingly, any deciduousness, whether synchronous or not, slowed stem increment. More interestingly, the effect was immediately detected upon the subsequent census. This could indicate that stem diameter increment in these species depended on recently fixed carbon unavailable during leafless periods or that stored resources were directed elsewhere such as rebuilding leaf tissue (Latt *et al.* 2001). Hormonal stem diameter increment regulation mediated by leaves could also have been disrupted during the leafless periods.

Another consistent pattern we observed was the lack of correlation between reproductive phenology and stem diameter increment.

The amount of resources directed to reproductive activities might be masked by the size of the resource pool consumed by stem diameter increment or leaf flushing. In some species such as *D. panamensis*, flowering occurred coincident with the peak of new leaf production, so the drain on resources dedicated to the production of nonphotosynthetic organs might be offset by the higher photosynthetic capacity of new leaves. Alternatively, the effect of reproductive activity on stem diameter increment may have been too small to detect by our methods, or in species such as *D. panamensis*, in which flowers and fruit are produced over a long period of time, any effect of reproduction on stem diameter increment would have been spread over several months making detection of the magnitude of the effect difficult. Nevertheless, we did not detect any effect of flowering and fruiting on stem diameter increment in the evergreen and deciduous species where leaf flushing or leaf turnover did not directly coincide with reproduction, indicating that the amount of energy

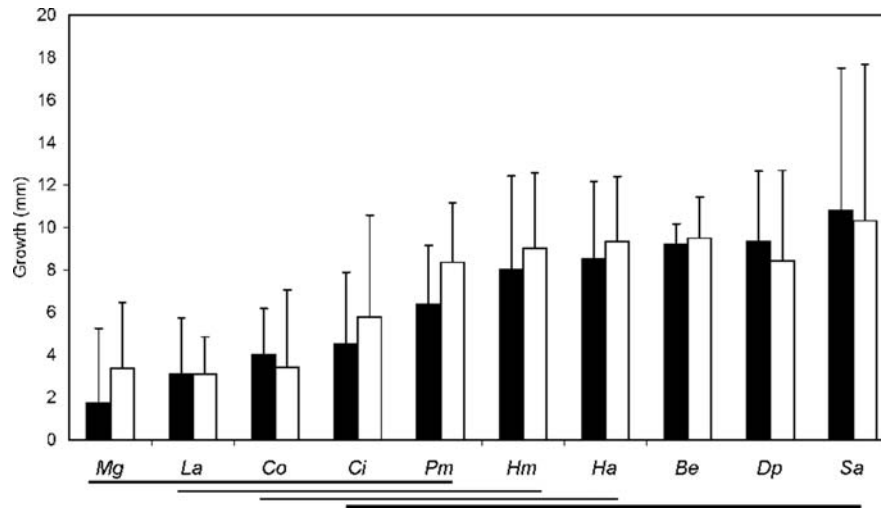


FIGURE 3. Mean growth of the ten species. The solid bars represent growth from August 1997 to July 1998, and the open bars represent growth from August 1998 to July 1999. The vertical lines are 1 SD. There was no difference in growth rates between the 2 yr ($P > 0.05$). Species that did not differ at $\alpha = 0.05$ are marked by the four lines under the x-axis.

trees diverted to these activities might not have been sufficient to slow stem diameter increment.

Stem diameter increment in several evergreen taxa was nearly continuous, with brief periods of slower increases in stem diameter increment but with no obvious periods of dormancy. In contrast to this study, Hazlett (1987) and Breitsprecher and Bethel (1990) found long periods of dormancy in *H. mesoamericanum*, and *P. macroloba* growing in the same forest. The study period they reported on was not unusually dry or wet compared to our study period. The dormant periods observed by those authors were sufficiently long that we should have been able to detect them in a monthly census. Possibly, the lack of dormancy we observed was likely due to our selection of healthy, unshaded trees in the fastest growing size class. Older trees, trees with shaded canopies, or diseased trees might be expected to show periods of undetectable stem diameter increment or be more sensitive to weather conditions. Fichter *et al.* (2003) found evidence of rhythmic stem diameter increment through tree ring analysis in *P. macroloba*, and *M. guianensis*,

species in which we failed to observe any predictable stem diameter increment patterns. Their analysis was based on microscopic analysis of wood anatomy and morphology, observed over many decades of stem diameter increment. Since our study was short in duration and occurred during a period of very weak seasonality, subtle stem diameter increment differences might have gone undetected though our results did support their findings for *D. panamensis*, *H. mesoamericanum*, and *S. amara*. Perhaps monthly measurements using Liming style band dendrometers might not be sufficiently precise to capture brief or minute periods of dormancy.

Maximizing the capture of light could be one of the most important factors driving the phenology of rain forest trees (Van Shaik *et al.* 1993, Wright & van Shaik 1994, Saleska *et al.* 2003). *Simarouba amara* flushed new leaves that became fully expanded simultaneously with the highest light period. These young leaves might have higher assimilation rates than older, senescent leaves (Ackerly 1996, Wilson *et al.* 2000, Kitajima *et al.* 2002). The cost of new leaf production immediately prior to the high light period could explain the concurrent dip in stem diameter increment, but the new, efficiently photosynthesizing leaves might explain the subsequent rapid increase in stem diameter increment rates.

Using cost-benefit analysis, Kikuzawa (1991) predicted that evergreen plants are favored under weakly seasonal conditions such as those found at our study site, and deciduousness becomes more common as seasonality becomes more pronounced. Indeed, in the weakly seasonal environment of La Selva, the majority of canopy trees are evergreen, but deciduous species are not uncommon, especially in emergent taxa. These species had stem diameter increment rates equivalent to or greater than evergreen taxa (Fig. 3). If maximizing light capture is so important, why then would deciduous species persist in this weakly seasonal environment, and turnover leaves during the period of highest light levels? Old leaves are shed immediately after the period of highest irradiance in the deciduous

TABLE 2. Results of logistic regression on crown status and growth for each species. The crown status represented whether or not the crown was fully occupied by leaves (>75% cover) the month prior or the month of stem measurement. Positive coefficients indicate that there was a greater chance that a tree with a full crown grew better than average. The exponentiation of the B coefficient represents the log-likelihood ratio.

Species	B	SE	Wald	df	P	Exp(B)
<i>Balizia elegans</i>	0.85	0.48	3.20	1	0.074	2.35
<i>Lecythis ampla</i>	0.97	0.39	6.20	1	0.013	2.64
<i>Hymenolobium mesoamericanum</i>	2.23	0.35	40.9	1	0.000	9.29
<i>Dipteryx panamensis</i>	1.47	0.40	13.4	1	0.000	4.35

taxa *D. panamensis* and *L. ampla*. If maximizing light capture were driving phenology in these taxa, leaflessness during the annual period of lower light would minimize the impact of reduced photosynthesis by a leafless or partially leafless canopy. This would also maximize the amount of time for leaf expansion and chloroplast development prior to high light conditions, but also would expose the leaves to herbivores, physical damage, or pathogens for a longer period prior to months with higher light. More likely, leaflessness in these and other taxa with similar leaf phenology could be a mechanism for drought avoidance (Fetcher *et al.* 1994). The pattern of stem increment response seen in the evergreen *C. insignis* could be evidence of a high sensitivity to water stress in this species as the smallest increments were always coincident with the driest months. Light limitation would not explain this pattern since the driest portion of the year at La Selva coincides with the period of maximum irradiance. The results of Pereira da Silva *et al.* (2002) showed that tree stem diameter increment tracked rainfall in an Amazonian forest, but whether this was an impact of water stress of light cannot be determined. Nonetheless, if trees do not have access to permanent water supplies, avoiding water stress might explain leaflessness whether or not drought itself was the cue. Leaf shedding in *D. panamensis* and *L. ampla* was coincident with the period when drought stress would be most acute and would offer a mechanism to escape moisture stress. Emergent species such as these would be especially susceptible to drought stress, since their canopies are tightly coupled with the atmosphere (O'Brien *et al.* 2004). The tight coupling makes these species particularly sensitive to catastrophic xylem failure that might occur during the drier months (Tyree & Sperry 1988). Whether driven by exogenous or endogenous cues, an increase in leaf turnover during the drier season is likely a general response; leaf litterfall at La Selva peaks during the highest light period (D.A. Clark, unpubl. data).

Although maximizing light capture and/or avoiding drought have been identified as driving phenology in the tropics, leaf construction costs, photosynthetic capacity, and the relationship between photosynthetic efficiency and leaf age also can affect phenological patterns (Kikuzawa 1995, Ackerly 1996). Asynchronous leaf turnover, as seen in *B. elegans* and *H. mesoamericanum*, might be a mechanism to avoid herbivory by minimizing the amount of palatable leaves of a species present in the forest at any one time (Janzen 1975, Van Shaik *et al.* 1993). In addition, seasonal leaf drop could be a result of phylogenetic inertia in some of the deciduous species, such as species in the genera *Dipteryx* and *Lecythis*, whose center of diversity occurs in the central and northern Amazon, where the climate is more seasonal. This is unlikely in the case of *Lecythis*, since there are some evergreen species that co-occur with deciduous species in the Amazon, suggesting the evolution of different strategies. Information on the phenology of all the *Dipteryx* species is incomplete so the plasticity of leaf turnover in this genus cannot be assessed.

We could not identify a single trigger driving the seasonal rhythms in phenology and stem increment observed at La Selva, a pattern that has been seen elsewhere in the tropics (Wright & Cornejo 1990). Whether the species were responding to rainfall, light levels, or some combination of these or other parameters, at

least a portion of the species were likely reacting to some exogenous cues. One of the common predictions of general circulation models is a change in the degree and patterns of seasonality in the tropics; the climate of Central America and elsewhere is predicted to have greater seasonal variability in soil moisture, driven by changes in rainfall patterns (Hulme & Viner 1998). The degree of plasticity in tropical tree phenological response to changing climatic cues is unknown, but is high in temperate species (Chuine *et al.* 2000). While phenological plasticity could also be high in the tropics, large climatic changes could still affect the relative competitive ability of species with different phenological strategies. Alteration in the pattern of seasonal irradiance could cause a shift in forest composition as the relative competitive ability of deciduous and evergreen species shifted. If plasticity of tropical tree phenology were low, the effects of any changes in climatic seasonality on tropical forests would be magnified. If rainfall and irradiance become more seasonal, deciduous species might become more abundant.

Investigations of tree stem diameter increment, carbon cycling, and climate change in wet tropical forests must consider the interaction of climate and phenology on tree and forest carbon dynamics. In this study, both seasonally and nonseasonally deciduous species grew less after leaf flush. An investigation of the correlation between climate and stem diameter increment would be hidden by slowed stem diameter increment driven by responses to leaf phenology, not by a direct effect of climate during these periods of leaflessness. Depending on the proportion of deciduous taxa in a forest, the relationship between whole forest carbon uptake and climate could become partially decoupled especially if species were responding to only one or few environmental cues. This effect would be magnified if increased seasonality occurs and deciduous taxa became more dominant in areas currently occupied by evergreen tropical forests.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp
Table S1. *Species from the La Selva old-growth forest included in this study.*

Figure S1. Plots of leaf phenology of the deciduous species. Individual lines within each plot are observations from each of eight trees.

Figure S2. Standard scores of monthly growth increment of deciduous species. The bars represent SE.

Figure S3. Standard scores of monthly growth increment of evergreen species. The bars represent SE.

LITERATURE CITED

- ACKERLY, D. D. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. *In* S. S. Mulkey, R. L. Chazdon, and A. P. Smith (Eds.). *Tropical forest plant ecophysiology*, pp. 619–658. Chapman & Hall, London, UK.
- ASHTON, P., T. J. GIVNISH, AND S. APPANAH. 1988. Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44–66.
- BORCHERT, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15: 81–89.
- BORCHERT, R. 1992. Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical forests. *Biotropica* 24: 385–395.
- BORCHERT, R. 1998. Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change* 39: 381–393.
- BORCHERT, R., AND G. RIVERA. 2001. Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiol.* 21: 213–221.
- BORCHERT, R., S. S. RENNER, Z. CALLE, D. NAVARRETE, A. TYE, L. GAUTIER, R. SPICHTIGER, AND P. VON HILDEBRAND. 2005. Photoperiodic induction of synchronous flowering near the Equator. *Nature* 433: 627–629.
- BREITSPRECHER, A., AND J. S. BETHEL. 1990. Stem-growth periodicity of trees in a tropical wet forest of Costa Rica. *Ecology* 71: 1156–1164.
- BULLOCK, S. H. 1997. Effects of seasonal rainfall on radial growth in two tropical tree species. *Int. J. Biometeorol.* 41: 13–16.
- CHUINE, I., J. BELMONTE, AND A. MIGNOT. 2000. A modelling analysis of the genetic variation of phenology between tree populations. *J. Ecol.* 88: 561–570.
- CLARK, D. A., AND D. B. CLARK. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecol. Monogr.* 62: 315–344.
- CLARK, D. A., AND D. B. CLARK. 1999. Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. *Ecol. Appl.* 9: 981–997.
- CORLETT, R. T., AND J. V. LAFRANKIE, JR. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change* 39: 439–453.
- FETCHER, N. S., S. F. OBERBAUER, AND R. L. CHAZDON. 1994. Physiological ecology of trees, shrubs, and herbs at La Selva. *In* L. A. McDade, K. S. Bawa, H. A. HESPENHEIDE, AND G. S. HARTSHORN (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 128–141. University of Chicago Press, Chicago, Illinois.
- FICHTLER, E., D. A. CLARK, AND M. WORBES. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ¹⁴C. *Biotropica* 35: 306–317.
- FORSYTHE, W. C., E. J. RYKIEL JR., R. S. STAHL, H. WU, AND R. M. SCHOOLFIELD. 1995. A model comparison for daylength as a function of latitude and day of year. *Ecol. Model.* 80: 87–95.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- GRAHAM, E. A., S. S. MULKEY, K. KITAJIMA, N. G. PHILLIPS, AND S. J. WRIGHT. 2003. Cloud cover limits net CO₂ uptake and growth of a rain forest tree during tropical rainy seasons. *Proc. Natl. Acad. Sci. USA* 100: 572–576.
- HAZLETT, D. L. 1987. Seasonal cambial activity for *Pentaclethra*, *Goethalsia*, and *Carapa* trees in a Costa Rican lowland forest. *Biotropica* 19: 357–360.
- HULME, M., AND D. VINER. 1998. A climate change scenario for the tropics. *Climatic Change* 39: 145–176.
- JANZEN, D. H. 1975. *Ecology of plants in the tropics*. The Institute of Biology's Studies in Biology, no. 58. Edward Arnold, London, UK.
- KEELAND, B. D., AND R. R. SHARITZ. 1993. Accuracy of tree growth measurements using dendrometer bands. *Can. J. For. Res.* 23: 2454–2457.
- KIKUZAWA, K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographic pattern. *Am. Nat.* 138: 1250–1263.
- KIKUZAWA, K. 1995. Leaf phenology as an optimal strategy for carbon gain in plants. *Can. J. Bot.* 73: 158–163.
- KIMURA, K., T. YUMOTO, AND K. KIKUZAWA. 2001. Fruiting phenology of fleshy-fruited plants and seasonal dynamics of frugivorous birds in four vegetation zones on Mt. Kinabalu, Borneo. *J. Trop. Ecol.* 17: 833–858.
- KING, D. A. 1996. Allometry and life histories of tropical trees. *J. Trop. Ecol.* 12: 25–44.
- KITAJIMA, K., S. S. MULKEY, M. SAMANIEGO, AND S. J. WRIGHT. 2002. Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. *Am. J. Bot.* 89: 1925–1932.
- LATT, C. R., P. K. R. NAIR, AND B. T. KANG. 2001. Reserve carbohydrate levels in the boles and structural roots of five multipurpose tree species in a seasonally dry tropical climate. *For. Ecol. Manage.* 146: 145–158.
- LAURANCE, W. F., J. M. RANKIN-DE MERONA, A. ANDRADE, S. G. LAURANCE, S. D'ANGELO, T. E. LOVEJOY, AND H. L. VASCONCELOS. 2003. Rain-forest fragmentation and the phenology of Amazonian tree communities. *J. Trop. Ecol.* 19: 343–347.
- LEIGH, E. G., JR. 1999. *Tropical forest ecology: A view from Barro Colorado Island*. Oxford University Press, New York, New York.
- LIMING, F. G. 1957. Homemade dendrometers. *J. For.* 55: 575–577.
- MEDINA, E. 1983. Adaptations of tropical trees to moisture stress. *In* F. B. Golley (Ed.). *Tropical rain forest ecosystems: Structure and function*, pp. 225–237. Elsevier, Amsterdam, The Netherlands.
- MCDADE, L. A., K. S. BAWA, H. A. HESPENHEIDE, AND G. S. HARTSHORN. 1994. *La Selva: Ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago, Illinois.
- NEWSTROM, L. E., G. W. FRANKIE, AND H. G. BAKER. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26: 141–159.
- O'BRIEN, J. J., S. F. OBERBAUER, D. B. CLARK, AND D. A. CLARK. 2004. Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. *Plant Cell Environ.* 27: 551–567.
- PEREIRA DA SILVA, R., J. DOS SANTOS, E. S. TRIBUZY, J. Q. CHAMBERS, S. NAKAMURA, AND N. HIGUCHI. 2002. Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *For. Ecol. Manage.* 166: 295–301.
- REICH, P. B. 1995. Phenology of tropical forests: Patterns, causes and consequences. *Can. J. Bot.* 73: 164–174.
- SALESKA, S. R., S. D. MILLER, D. M. MATROSS, M. L. GOULDEN, S. C. WOFSY, H. R. DA ROCHA, P. B. DE CAMARGO, P. CRILL, B. C. DAUBE, H. C. DE FREITAS, L. HUTYRA, M. KELLER, V. KIRCHHOFF, M. MENTON, J. W. MUNGER, E. H. PYLE, A. H. RICE, AND H. SILVA. 2003. Carbon in Amazon forests: Unexpected seasonal fluxes and disturbance-induced losses. *Science* 302: 1154–1157.
- SCHÖNGART, J. M., T. F. PIEDADE, S. LUDWIGSHAUSEN, V. HORNA, AND M. WORBES. 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *J. Trop. Ecol.* 18: 581–597.
- SYKES, J. M., A. D. HERRILL, AND M. D. MOUNTFORD. 1983. Use of visual cover estimates as quantitative estimators of some British woodland taxa. *J. Ecol.* 71: 437–450.
- TYREE, M. T., AND J. S. SPERRY. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88: 574–580.
- VAN SHAIK, C. P., J. W. TERBORG, AND S. J. WRIGHT. 1993. Phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353–377.
- WALTER, H. 1985. *Vegetation of the earth and ecological systems of the geobiosphere*. 3rd edition. Springer-Verlag, New York, New York.
- WILSON, K. B., D. D. BALDOCCHI, AND P. J. HANSON. 2000. Quantifying stomatal and non-stomatal limitations to carbon assimilation resulting

- from leaf aging and drought in mature deciduous tree species. *Tree Physiol.* 20: 787–797.
- WORBES, M. 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo forest reserve in Venezuela. *J. Ecol.* 87: 391–403.
- WRIGHT, S. J., AND E. H. CORNEJO. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71: 1165–1175.
- WRIGHT, S. J., AND C. P. VAN SHAIK. 1994. Light and the phenology of tropical trees. *Am. Nat.* 143: 192–199.