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RELATIONSHIPS AMONG TIME, FREQUENCY, AND DURATION OF FLOWERING IN TROPICAL RAIN FOREST TREES¹

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Flowering patterns are defined by the timing, duration, and frequency of flowering. Plants, particularly in the tropics, vary enormously with respect to these main variables of flowering. We used data from 302 tree species in a wet tropical forest to test a series of predictions regarding timing, duration, and frequency of flowering and examined the effect of each variable on the other two. Because timing, duration, and frequency of flowering can be constrained by phylogeny, we analyzed the data before and after considering phylogenetic effects at the level of family. Flowering activity peaked in the first wet season from May to July, refuting our prediction of peak flowering during the dry season. Our prediction that most species should flower several times a year was supported when species flowering more or less continually throughout the year were included in this category. Our prediction that supra-annually flowering species should be the least frequent was also supported with some qualifications. As we predicted, species flowering several times a year bloomed relatively briefly per flowering episode. Our prediction of shorter flowering duration for species flowering in the dry season and for those with a temporal separation between flowering and vegetative growth was also supported. Furthermore, supra-annually flowering species flowered for a shorter duration than annually flowering species and had a higher probability of flowering in the dry season compared to episodically or annually flowering species. Phylogeny significantly constrained variation in flowering frequency, but not in flowering time or duration, among confamilial species.

Key words: Costa Rica; flowering patterns; flowering phenology; phylogeny; tropical forests.

The timing, duration, and frequency of flowering define flowering patterns. Plants display a wide variety of patterns, particularly in aseasonal tropics, where favorable conditions for flowering throughout the year result in a broad range of variation in timing, frequency, and duration of flowering (Gentry, 1974a, b; Bawa, 1983; Newstrom et al., 1994a, b, and references therein). Species in the tropics can potentially flower any time of the year, yet coexisting species vary considerably with respect to timing of flowering (Janzen, 1967; Bawa, 1983). Similarly, the frequency of flowering ranges from several times a year to once in several years (Frankie et al., 1974; Bullock et al., 1983; Appanah, 1993; Sakai et al., 1999). Tropical species in the same community also vary enormously in duration of flowering, from a few days to the whole year (Gentry, 1974a; Opler et al., 1980).

In outcrossing plants, flowering patterns determine the outcome of selection by influencing the amount of outcrossing (Koptur, 1984; Murawski and Hamrick, 1991), number of mates (Bawa, 1983), near-neighbor matings (Chase et al., 1996), and reproductive output (Janzen, 1974). Yet little is known about constraints on the timing, duration, or frequency of flowering, and the selective forces that shape the evolution of various patterns. One possible reason for this neglect is that the diversity of flowering patterns is greatest in aseasonal tropics, where patterns have not been fully described.

The extensive literature on flowering phenology of tropical plants is largely focused on the timing or seasonality of flowering at the community level (Janzen, 1967; Frankie et al., 1974; Opler et al., 1980; Wright and Calderon, 1995). Except

for supra-annual flowering (Janzen, 1974; Appanah, 1985, 1993, and references therein), little attention has been paid to the frequency of flowering (but see Newstrom et al., 1994a, b). The duration of flowering has received virtually no attention, although some authors provide classification schemes including the concept of duration such as mass vs. extended or seasonal vs. extended (Frankie et al., 1974; Gentry, 1974a; Bawa, 1983).

Furthermore, timing, duration, and frequency of flowering have been examined in isolation from one another. However, there are reasons to assume that these three parameters interact with each other to shape the diversity of flowering patterns we observe in nature (see below). However, such interactions among timing, duration, and frequency and the outcomes of such interactions have not been explored before.

Here, we test a number of predictions concerning timing, duration, and frequency of flowering and how these variables are interrelated. These predictions emerge from various hypotheses about the evolution of flowering patterns, but have rarely been explicitly tested in a comprehensive manner. Tests of predictions allow new insights into abiotic and biotic forces that shape flowering patterns. In this paper, our focus is on the timing, duration, and frequency of flowering and the influence of each parameter on the other two. In a subsequent paper, we examine how timing, duration, and frequency are correlated with successional status, habit, sexual systems, and pollinators.

Several predictions can be made about the timing, duration, and frequency of flowering on the basis of abundance and allocation of resources. First, with respect to timing, Janzen (1967) suggested that tree species in dry tropical forest should flower in the dry season because the wet season is the major period for vegetative growth for these species. Reproduction in the dry season allows temporal separation of reproductive activity and vegetative growth. Janzen also attributed a major role to pollinators as selective agents. Most dry-forest trees are

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pollinated by a diverse range of bees that are seasonally abundant, and the lack of leaves in the dry season may increase the visibility of flowers to pollinators (Janzen, 1967; Daubenmire, 1972; Frankie et al., 1983). According to Borchert (1980, 1983), water stress is a major impetus for flowering during the dry season. In aseasonal tropics, there is no pronounced dry season. Nevertheless, if the factors postulated by Janzen and Borchert are operating, one should expect more species to flower during the periods of low rainfall than during the wet season.

With respect to frequency, in order to maximize lifetime reproductive output, species that flower several times a year should be more common than species that flower annually, which in turn should be more abundant than species that flower supra-annually. In reference to duration, tropical forest species can flower basically throughout the year. However, on the basis of energetics, species that flower several times a year should flower for a shorter period than annually flowering species because fruit formation often interferes with flowering (Bawa, 1983; Rathcke and Lacey, 1985). Thus, in annually flowering species, flowering and fruiting can occur over a longer period than in episodically flowering species.

With respect to interaction among timing, duration, and frequency of flowering, supra-annual species should flower for a shorter period and in the dry season. Such species, during their flowering, attract pollinators from other species or assist in building up pollinator faunas in those cases where many species in the community participate in supra-annual flowering (Ashton et al., 1988; Appanah, 1993). To attract or build up pollinators, massive floral displays over a short period are required. Environmental cues are required to trigger supra-annual flowering (Ashton et al., 1988). Such cues may be more effective in the dry than in the wet season because relatively abundant moisture in the wet season diminishes environmental fluctuation in temperature as well as water stress. Species in which growth and reproduction is separated over time should also flower for shorter periods than species in which vegetative growth and reproduction occur simultaneously. Thus, by inference, duration of flowering in species that bloom during the dry season when vegetative growth may be minimal should be shorter than that for wet season species.

In summary, our predictions are as follows: (1) Most tree species in aseasonal tropics should flower during the period with the lowest rainfall. (2) Species that flower several times a year should be most abundant, and supra-annual species least abundant. (3) Species that flower several times a year should bloom for the shortest period per flowering episode. (4) Species that flower during the dry season or species in which there is a temporal separation of flowering and vegetative growth should flower over a shorter period than species in which there is no such decoupling. (5) Flowering in supra-annual species should be shorter than in annually flowering species and should occur during the dry season.

It is important to emphasize that these predictions are based on the assumption that everything else in the natural history of the various species in the community is the same, which we know is not the case. Yet, as we will show, results of our analyses remarkably conform to the predictions and reveal additional general trends not noticed before.

MATERIALS AND METHODS

Flowering phenology of tree species (302 species from 58 families) was observed at the La Selva Biological Station of the Organization for Tropical

Studies in Costa Rica for 3 yr (1978–1980). This Biological Station, encompassing 1536 ha, is located in the province of Heredia, Costa Rica (10°20' N, 83°59' W), and includes a typical tropical wet forest with an annual rainfall of 4000 mm. A total of 1458 native species and 220 exotic species have been identified (Lieberman and Lieberman, 1994). Herbs are most common (35%), followed by epiphytes (23%), trees (20%), shrubs (17%), and lianas (6%) (Hartshorn and Hammel, 1994). Clark (1994) also showed that in 12.4 ha of the primary forest in La Selva the overall density is less than one individual (dbh > 10 cm) for 70% of the tree and liana species.

Flowering time, frequency, and duration were noted at weekly intervals for tree species along trails. More than 1000 individuals belonging to 302 species of 58 families were marked along the trails of the station. One to several flowering trees were observed with binoculars for each species: one (18.8%), few (2–4 trees, 38.6%), several (5–10 trees, 23.3%) and many (10+ trees, 19.3%). Since flowering in 1979 was quite poor, data were analyzed for observations made in 1978 and 1980, except where indicated otherwise.

Many species at La Selva flowered for several months or several times a year, and the month of flowering of these species varied within a range from year to year. Thus, the month of flowering for these species was obtained from data pooled over 3 yr. Flowering time for each species was then categorized into four levels primarily on the basis of seasonality, in particular, flowering in the “first wet” (May–July), “second wet” (November–January), and “dry” (the rest of the months) season. “First-wet” consists of species that flower during the first wet season but do not flower during the second wet season. “Second-wet” consists of those species that flower in the second wet season, but not in the first. “Both-wet” includes species that flower in the first or second wet season or from the first to the second wet seasons during a year. “Dry” includes species that flower only in the dry season. Our description of wet seasons follows the differentiation by Newstrom et al. (1994b) who recently analyzed long-term phenological records of La Selva trees.

Flowering frequency was classified into four levels based on flowering frequency per year: continual species that flower more or less continually during a year, episodic species that flower more than once a year, annual species that flower once a year, and supra-annual species that flower less frequently than once a year. Episodically flowering species flower from two to six times a year (sub-annual flowering frequency). Our observations most likely reflect the minimum number of episodes within a year. The interval between flowerings was not determined for any supra-annually flowering species in this study.

The flowering duration (in weeks) is an approximate length of the flowering per typical episode. If flowering duration varied within a range, maximum values were used for each species. For species in which flowering lasted less than 1 wk, 1 wk was noted as the duration of flowering. Throughout this paper, flowering duration indicates duration per episode if not mentioned otherwise. For episodically flowering species that repeat flowering during a year, a yearly duration was obtained by multiplying duration per episode with the frequency of sub-annual flowering.

The species number in a family varied greatly among all 58 families listed: 14 families with one species each, 10 families with two species, 10 families with three species, seven families with four species, two families with five species, and 15 families with six or more species.

We first describe characters such as flowering time, frequency, and duration among La Selva trees. Then we evaluate the relationship between each flowering character and phylogeny at the level of family. Finally, we examine the relationship among the three flowering characters without considering phylogeny. For the last analysis, data was pooled from all 58 families.

The relationship between categorical variables such as flowering time and frequency was tested using two-way contingency table analyses. The adjusted standardized residuals were examined to identify the categories contributing significantly to the *G* value. Flowering duration, unlike flowering time and frequency, was treated as a continuous variable to extract quantitative information on variation in duration. The relationships between duration and both flowering time and frequency were tested separately as well as simultaneously using one- and two-way ANOVAs with flowering duration as the dependent variable.

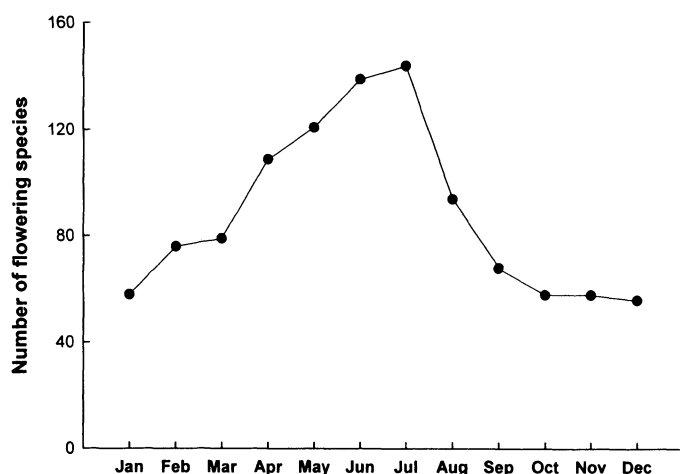


Fig. 1. Number of flowering tree species during each month of the year. Flowering time of a species varied within a range, and the month of flowering was pooled over 3 yr (1978–1980).

In order to consider the effect of phylogeny on the associations between pairs of flowering characters, two different analyses were conducted. A three-way contingency table analysis (flowering time \times frequency \times phylogeny) could not be performed because a skewed distribution of species across families contributed to a violation of the assumption of less than 20% of the cells with expected counts less than five (Marascuilo and Levin, 1983). Thus, the association between flowering time and frequency, independently of phylogeny, was examined based on subset data of 43 minor families. Each of these minor families contained five or fewer species with a mean of 2.37 (SD = 1.24) species per family. We assumed that in the subset data the effect of phylogeny was not large enough to change the relationship between flowering time and frequency. For analyses involving flowering duration, phylogeny was incorporated as a class variable in ANOVAs. Data of species in seven large families (Annonaceae, Euphorbiaceae, Lauraceae, Leguminosae, Moraceae, Palmae, and Rubiaceae) comprising 47.4% of the total species examined were used in ANOVAs.

Finally, the relationship between flowering duration and flowering time, frequency, and phylogeny was simultaneously examined in ANOVA with the latter three characters as class variables. With an assumption of no three-way interaction of flowering time \times frequency \times phylogeny regarding flowering duration, two-way interaction terms of flowering time and frequency and phylogeny were incorporated into the three-way ANOVA. ANOVAs were tested with the type III SS (GLM procedure: SAS, 1982). Species flowering continually ($N = 15$) with no variation in flowering duration were omitted from analyses of variance. Flowering duration was \log_{10} transformed to meet the assumption of normality. Means of flowering duration are given with 1 SD throughout this paper.

RESULTS

Description of flowering characters—The number of flowering species varied widely among months of the year (Fig. 1) and was the highest in July (49.0%) and lowest in December (19.0%). When the months were grouped into four periods (February–April, May–July, August–October, November–January), the mean number of species in flower was not equal across the periods ($G = 26.96$, $df = 3$, $P < 0.001$). The quadratic model also did not fit the periodicity of species in flower (Fig. 2: $G = 6.50$, $df = 1$, $P < 0.05$), because the observed number in flowering species was higher during May–July and lower during August–October than expected.

When flowering time of each species was categorized according to the seasons, more than half of the observed trees

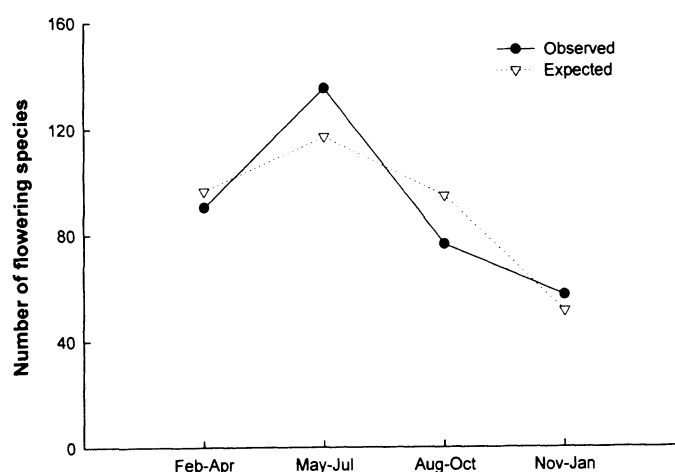


Fig. 2. Seasonal pattern of flowering tree species. Observed values are seasonal mean number of flowering species, while expected values were obtained based on a quadratic model. The quadratic model did not fit the observed seasonal pattern. The four seasons were divided following Newstrom et al. (1994b).

were found to flower in the first-wet season (156 of 294 species). The fewest species flowered in the second-wet season. Thus, the proportion of species flowering in each season decreased in order of first-wet season (53.1%) > both-wet season (21.1%) > dry season (16.0%) > second-wet season (9.9%). Because flowering time is based on data pooled by month for 3 yr and the month of flowering can vary each year, most species belonging to the first-wet, second-wet, and both-wet categories flowered in the dry season as well. For example, about 78% of the species flowering in the first-wet season also flowered in the dry season during the 3 yr.

Among 241 tree species in La Selva for which we had information on flowering time, frequency, and duration, species flowering annually or episodically were more abundant (42.3 and 37.3%, respectively) than those flowering supra-annually or continually (14.1 and 6.2%, respectively). In episodically flowering species, episodes varied from two to six per year. However, the sub-annual flowering frequency was skewed to the right tail: 80.6% of species with episodic mode flowered twice or three times a year (Fig. 3).

With the exception of species that flowered more or less continually during a year, flowering duration varied widely with a mean of 5.58 ± 0.99 wk ($N = 204$). For example, *Cassipourea elliptica* (Rhizophoraceae), *Cestrum racemosum* (Solanaceae), and *Rollinia pittieri* (Annonaceae) flowered for 1 wk or less, but at the other extreme, *Colubrina spinosa* (Rhamnaceae) flowered for 40 wk. Overall, one-third of the species flowered for a month or less and another third between 1 and 2 mo (Fig. 4).

Relationship between phylogeny and flowering characters—*Phylogeny and flowering time*—Flowering time was not associated with phylogeny (Table 1). Regardless of family membership, the proportion of flowering species decreased in order of first-wet, both-wet, dry, and second-wet seasons. More than 50% of the species flowered actively in the first-wet season.

Phylogeny and flowering frequency—Flowering frequency was strongly associated with phylogeny (Table 1). For exam-

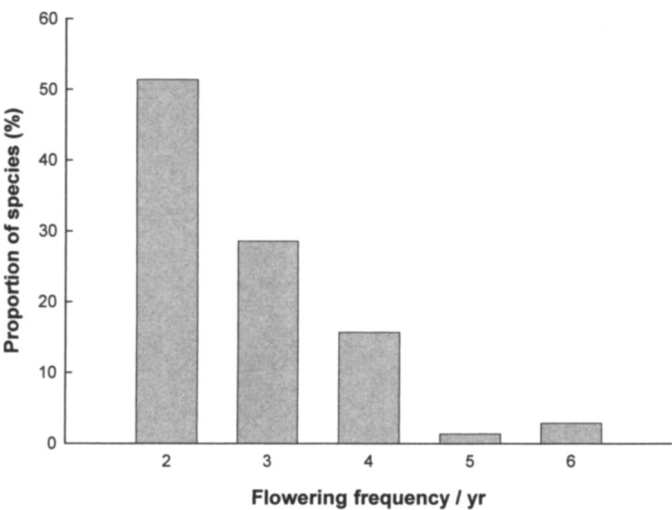


Fig. 3. Proportion of episodically flowering species with different flowering frequencies per year. $N = 70$.

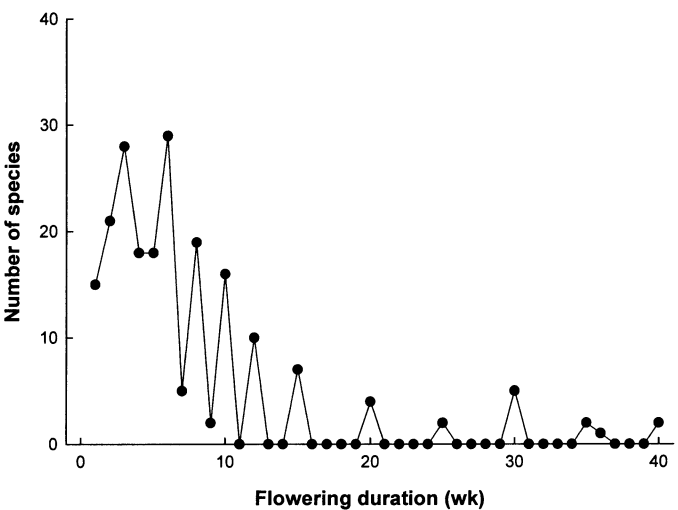


Fig. 4. Frequency distribution of flowering duration among tropical rain forest trees at La Selva ($N = 204$). Species that flowered more or less continually throughout the year were not included ($N = 15$).

ple, more species of the Moraceae flowered episodically (76.9%) relative to other families. Similarly, 75% of species in the Lauraceae flowered annually, and four of 15 of the continually flowering species belonged to the Rubiaceae. However, among episodic species in the seven large families, the frequency of sub-annual flowering (with three levels: two, three, and four or more times a year) was independent of phylogeny ($G = 9.68$, $P \gg 0.05$, $df = 10$, N [total] = 37).

Phylogeny and flowering duration—The duration of flowering in the Annonaceae lasted twice as long as in the Leguminosae (Table 2). However, mean duration did not differ among the seven large families (Table 2). The range of the mean duration may increase to some extent for some families comprising continually flowering species such as Rubiaceae and Annonaceae, though these families had small numbers of continually flowering species ($N = 4$ and 2, respectively).

Relationship between flowering characters—*Flowering time and frequency*—THE PATTERN BEFORE CONSIDERING PHYLOGENY—Flowering time and frequency (Table 3A) were significantly associated, even when species with continual flowering were excluded ($G = 44.66$, $P < 0.001$, $df = 6$). All of continually flowering species, by definition, flowered in both-wet seasons. Episodically flowering species were four times more likely to flower in both-wet seasons than were annually

flowering species. In contrast, none of the supra-annually flowering species flowered in both-wet seasons. Supra-annually flowering species were 4.3 and 2.2 times more likely to flower in the dry season than episodically and annually flowering species, respectively (Table 3A). However, 72.4% of supra-annually flowering species bloomed in the first-wet season.

THE PATTERN AFTER CONSIDERING PHYLOGENY—The two-way contingency table of flowering time \times frequency was highly significant for the subset data including 43 minor families (Table 3B). Supra-annually flowering species blooming in the dry season were 8.3 and 4.3 times more common than episodically and annually flowering species, respectively. The overall similarity of the results between Table 3A and 3B suggests that the association of flowering time and frequency does not accrue through a correlation of flowering frequency and phylogeny.

Flowering time and duration—THE PATTERN BEFORE CONSIDERING PHYLOGENY—Flowering time accounted for 11.3% of the total variance in flowering duration (Table 4A). Species flowering in different seasons demonstrated a 2.7-fold difference in mean flowering duration (Table 4A). For example, the species flowering in both-wet seasons bloomed for the longest period with a mean of 8.22 wk, followed by second-wet, first-

TABLE 1. Frequency of tree species at La Selva, Costa Rica, in two-way contingency tables of both flowering time and frequency and phylogeny. Likelihood ratio chi square (G) is reported for each two-way contingency table.

| Phylogeny | Flowering time | | | | G | Flowering frequency ^a | | | | G |
|---------------|----------------|------------|----------|-----|----------|----------------------------------|----------|--------|--------------|----------|
| | First-wet | Second-wet | Both-wet | Dry | | Continual | Episodic | Annual | Supra-annual | |
| Annonaceae | 8 | 0 | 3 | 1 | 12.21 ns | 2 | 5 | 3 | 1 | 41.99*** |
| Euphorbiaceae | 10 | 2 | 6 | 1 | | 1 | 8 | 6 | 1 | |
| Lauraceae | 8 | 1 | 1 | 4 | | 0 | 1 | 9 | 2 | |
| Leguminosae | 18 | 2 | 6 | 4 | | 0 | 14 | 8 | 5 | |
| Moraceae | 9 | 0 | 5 | 3 | | 1 | 10+ | 2 | 0 | |
| Palmae | 14 | 1 | 4 | 2 | | 0 | 5 | 10 | 0 | |
| Rubiaceae | 17 | 1 | 5 | 5 | | 4 | 5 | 10 | 5 | |

^a A + sign indicates where the observed value was greater than the expected value at $\alpha = 0.05$ level.
*** $P < 0.001$; ns = not significant.

TABLE 2. Means and standard deviations of flowering duration per episode (in weeks) among tree species of seven large families at La Selva, Costa Rica.

| Class variable | \bar{X} (wk) | SD | N |
|----------------|----------------|------|-----|
| Annonaceae | 7.23 | 2.10 | 9 |
| Euphorbiaceae | 4.91 | 1.60 | 13 |
| Lauraceae | 6.61 | 1.54 | 11 |
| Leguminosae | 3.52 | 2.04 | 25 |
| Moraceae | 5.13 | 1.73 | 13 |
| Palmae | 5.39 | 2.63 | 12 |
| Rubiaceae | 5.81 | 1.94 | 19 |

 $F_{6,95} = 1.42$ ns

ns = not significant.

wet, and dry season flowering species. The species flowering in both-wet and second-wet seasons displayed flowers for a significantly longer period than dry season flowering species, and first-wet season flowering species also tended to bloom longer than the latter.

THE PATTERN AFTER CONSIDERING PHYLOGENY—In the simultaneous test for effects of flowering time and phylogeny on flowering duration, the interaction effect of flowering time \times phylogeny was close to the level of significance (Table 4B). In separate analyses for each family, the effect of flowering time on flowering duration was marginally significant in the Palmae (Kruskal-Wallis one-way ANOVA: Annonaceae $\chi^2 = 2.44$, $df = 1$; Euphorbiaceae $\chi^2 = 1.32$, $df = 2$; Lauraceae $\chi^2 = 5.04$, $df = 3$; Leguminosae $\chi^2 = 4.59$, $df = 3$; Moraceae $\chi^2 = 0.80$, $df = 2$; Rubiaceae $\chi^2 = 3.78$, $df = 3$, $P > 0.05$ for all these families; Palmae $\chi^2 = 7.36$, $df = 3$, $P = 0.0614$). However, among families, the overall trend was toward longer flowering in the both-wet season flowering species, particularly compared to species flowering in the dry season (Fig. 5).

Flowering frequency and duration—THE PATTERN BEFORE CONSIDERING PHYLOGENY—Flowering frequency accounted for a slightly higher proportion of the variance in flowering duration (15.8%) than did flowering time (Table 5A). Mean flowering duration varied by a factor of 2.2 among species with different flowering frequencies (Table 5A). Both episod-

TABLE 3. Frequency of tree species at La Selva, Costa Rica, in a two-way contingency table of flowering time and frequency. Analyses were conducted twice based on data set A that included species of all families and set B that included species of 43 minor families. Likelihood ratio chi square (G) is reported for each two-way contingency table.

| Trait | Flowering time | | | | <i>G</i> |
|------------------------|----------------|------------|----------|-----|----------|
| | First-wet | Second-wet | Both-wet | Dry | |
| A) Flowering frequency | | | | | |
| Continual | 0– | 0 | 15+ | 0 | 88.61*** |
| Episodic | 41 | 8 | 35+ | 5 | |
| Annual | 65 | 15 | 10– | 11 | |
| Supra-annual | 21 | 1 | 0– | 7+ | |
| B) Flowering frequency | | | | | |
| Continual | 0 | 0 | 3+ | 0 | 30.26*** |
| Episodic | 12 | 4 | 8 | 1 | |
| Annual | 23 | 9 | 3 | 4 | |
| Supra-annual | 8 | 0 | 0 | 4+ | |

Note: A +/– sign indicates that observed values were greater or less than the expected values at $\alpha = 0.05$ level.

*** $P < 0.001$.

ically and supra-annually flowering species bloomed for a significantly shorter period than did annually flowering species.

When the effect of flowering frequency per year (with five levels, such as one, two, three, four, and five or more times a year) on flowering duration was examined, mean flowering duration per episode decreased as flowering frequency per year increased (Fig. 6). The relationship was highly significant ($F_{1,110} = 14.98$, $P < 0.001$, $R^2 = 12.0\%$). Statistical significance was detected only between species flowering once (annually flowering species) and those flowering at least twice and three times a year (Tukey's test: $P < 0.05$ for both pairs of test). However, because of repeated flowering during a year, episodically flowering species demonstrated a significantly longer mean for yearly flower duration than annually flowering species ($F_{1,158} = 6.51$, $P < 0.05$; $\bar{X} = 11.07 \pm 2.14$ week, $N = 70$ and 7.99 ± 2.00 wk, $N = 89$, respectively).

THE PATTERN AFTER CONSIDERING PHYLOGENY—The simultaneous effects of flowering frequency and phylogeny on

TABLE 4. (A) One-way ANOVA of the effect of flowering time and (B) two-way ANOVA of the effects of flowering time and phylogeny on flowering duration per episode among tree species at La Selva, Costa Rica. One-way ANOVA was conducted using species of all families, while two-way ANOVA was conducted using species of the seven large families. Multiple range tests were conducted following one-way ANOVA. A shared letter among categories of flowering time indicates no significant differences of means at $\alpha = 0.05$ level. Significance of factors was tested based on the Type III sums of squares.

| Source of variation | df | F | P | Categories of flowering time | \bar{X} (wk) | SD | N |
|-------------------------|-------|------|-----|------------------------------|--------------------|------|-----|
| A) | | | | | | | |
| Flowering time | 3,198 | 8.44 | *** | First-wet | 4.99 ^{BC} | 1.82 | 119 |
| | | | | Second-wet | 6.87 ^{AC} | 1.98 | 24 |
| | | | | Both-wet | 8.22 ^A | 2.24 | 41 |
| | | | | Dry | 3.08 ^B | 1.54 | 18 |
| B) | | | | | | | |
| Flowering time (Time) | 3 | 9.82 | *** | | | | |
| Phylogeny | 6 | 3.33 | ** | | | | |
| Time \times Phylogeny | 14 | 1.46 | (*) | | | | |
| Model | 23,77 | 2.44 | ** | | | | |

(*) $P = 0.1475$; ** $P < 0.01$; *** $P < 0.001$.

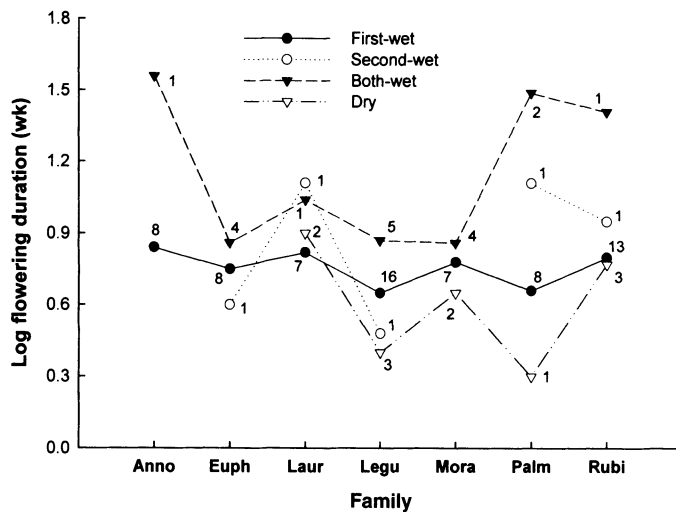


Fig. 5. Mean log flowering duration of each of seven large families, according to flowering time. Numbers by symbols represent the number of species in different classes of flowering time within each family. Anno = Annonaceae; Euph = Euphorbiaceae; Laur = Lauraceae; Legu = Leguminosae; Mora = Moraceae; Palm = Palmae; Rubi = Rubiaceae.

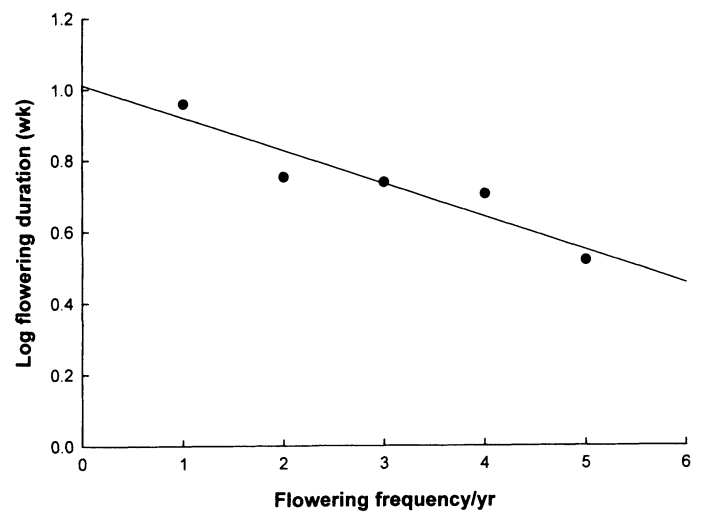


Fig. 6. Mean log of flowering duration among tropical rain forest trees at La Selva with varying flowering frequencies per year. Regression line shows the relationship between flowering frequency and duration. N for flowering one, two, three, four, and five times per year is 90, 36, 20, 11, and 3, respectively.

flowering duration were not significant (Table 5B). When the two variables were hierarchically included in the model, flowering frequency had significant effects on flowering duration regardless of the order in the model (flowering frequency first: $F_{2,76} = 4.32$; second: $F_{2,76} = 3.80$, $P < 0.05$ for both; phylogeny first: $F_{6,76} = 1.42$; second: $F_{6,76} = 1.25$, $P > 0.05$ for both). This result suggests that variation in flowering duration is directly related to flowering frequency rather than phylogeny.

Flowering duration, time, and frequency—THE PATTERN BEFORE CONSIDERING PHYLOGENY—The two-way model explained 37.8% of the variance in flowering duration (Table 6A). However, the effect of flowering time on the duration of flowering varied with flowering frequency (Table 6A). Separate analysis for each flowering frequency demonstrated that the effect of flowering time on duration was significant only in annually flowering species (episodic $F_{3,77} = 1.75$, $P > 0.05$; annual, $F_{3,85} = 21.69$, $P < 0.001$; supra-annual, $F_{2,19} = 0.13$,

$P > 0.05$). Among annually flowering species, species flowering in both-wet seasons bloomed for the longest period, followed by those flowering in second-wet, first-wet, and dry seasons (Fig. 7). All species flowering in the dry season, regardless of flowering frequency, flowered for less than 4 wk.

THE PATTERN AFTER CONSIDERING PHYLOGENY—When two-way interaction terms of flowering time, frequency, and phylogeny were incorporated into the three-way ANOVA with flowering time, frequency, and phylogeny as main factors, the final model accounted for 55.6% of the variance in flowering duration. Only flowering time had a significant effect (Table 6B). However, not only was sample size relatively small and uneven across cells, but also the interaction effect of flowering time \times phylogeny was relatively close to the level of significance ($P = 0.2173$). Thus, to build a conservative model to account for the variation of flowering duration, the effects of flowering time and phylogeny were tested separately for each flowering frequency. Neither of the main factors was signifi-

TABLE 5. (A) One-way ANOVA of the effect of flowering frequency and (B) two-way ANOVA of the effects of flowering frequency and phylogeny on flowering duration per episode among tree species at La Selva, Costa Rica. One-way ANOVA was conducted using species of all families, while two-way ANOVA was conducted using species of the seven large families. Multiple range tests were conducted following one-way ANOVA. A shared letter among categories of flowering frequency indicates no significant differences of means at alpha = 0.05 level. Significance of factors was tested based on Type III sums of squares.

| Source of variation | df | F | P | Categories of flowering frequency | \bar{X} (wk) | SD | N |
|----------------------------|-------|-------|-----|-----------------------------------|-------------------|------|----|
| A) | | | | | | | |
| Flowering frequency | 2,191 | 17.91 | *** | Episodic | 4.41 ^B | 1.98 | 81 |
| | | | | Annual | 7.99 ^A | 2.01 | 90 |
| | | | | Supra-annual | 3.68 ^B | 1.48 | 23 |
| B) | | | | | | | |
| Flowering frequency (Freq) | 2 | 2.62 | ns | | | | |
| Phylogeny | 6 | 0.99 | ns | | | | |
| Freq \times Phylogeny | 10 | 1.05 | ns | | | | |
| Model | 18,76 | 1.48 | ns | | | | |

*** $P < 0.001$; ns = not significant.

TABLE 6. (A) Two-way ANOVA of the effects of flowering time and frequency and (B) three-way ANOVA of the effects of flowering time, frequency, and phylogeny on flowering duration among tree species at La Selva, Costa Rica. Two-way ANOVA was conducted using species of all families, and three-way ANOVA was conducted using species of the seven large families. Significance of factors was tested based on Type III sums of squares.

| Source of variation | df | F | P | R ² |
|----------------------------|--------|-------|-----|----------------|
| A) | | | | |
| Flowering time (Time) | 3 | 15.82 | *** | 16.3 |
| Flowering frequency (Freq) | 2 | 21.65 | *** | 14.9 |
| Time × Freq | 5 | 4.95 | *** | 8.5 |
| Model | 10,181 | 11.02 | *** | 37.8 |
| B) | | | | |
| Flowering time (Time) | 3 | 7.10 | *** | 16.6 |
| Flowering frequency (Freq) | 2 | 2.07 | ns | |
| Phylogeny | 6 | 0.85 | ns | |
| Time × Freq | 3 | 1.53 | ns | |
| Time × Phylogeny | 11 | 0.36 | ns | |
| Freq × Phylogeny | 9 | 0.40 | ns | |
| Model | 36,57 | 1.98 | * | 55.6 |

* $P < 0.05$; *** $P < 0.001$; ns = not significant.

cant among episodically and supra-annually flowering species (Table 7; Fig. 8A, C). Flowering duration varied significantly with flowering time, but not with phylogeny, among annually flowering species (Table 7). Within annually flowering species, the difference in flowering duration was significant only between species flowering in both wet-seasons and those flowering in either one wet or the dry seasons ($P < 0.05$ for all pairs of tests; Fig. 8B).

Summary of results—Our results may be summarized as follows. The largest proportion of species in La Selva flowered in the first-wet season, followed by those flowering in both-wet, dry, and second-wet seasons. Episodically and annually flowering species were more abundant than continually and supra-annually flowering species. Species flowering supra-annually and those flowering in the dry season bore flowers for a brief period. Supra-annually flowering species were relatively dominant among dry-season flowering species. Among con-familial species, phylogeny strongly constrained variation in flowering frequency, but not in flowering time or duration. However, flowering frequency itself is not independent of flowering time and duration even after the effect of phylogeny was considered. For example, episodically flowering species, those that can reproduce several times a year, tended to flower during any season of the year with little variation in flowering duration. Supra-annually blooming species were likely to flower for a brief period either in the first wet or dry season. On

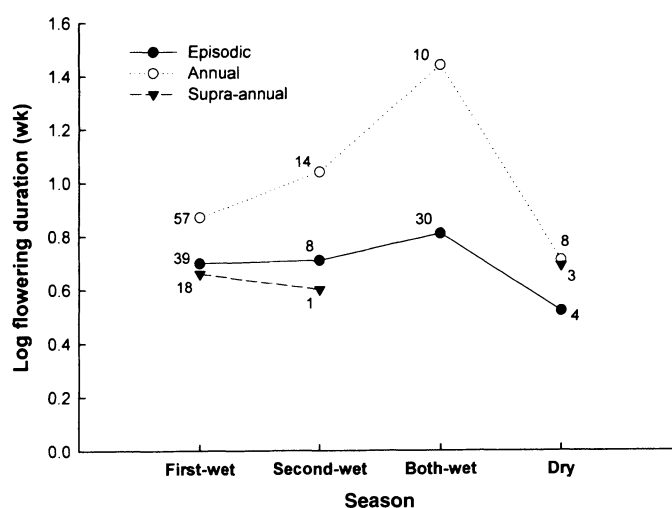


Fig. 7. Mean log of flowering duration for each class of flowering time, according to flowering frequency among species of all families. Numbers by symbols indicate the number of species in different classes of flowering time within each flowering frequency.

the other hand, annually flowering species flowered seasonally as well as aseasonally, exhibiting a wide range of variation in flowering duration.

DISCUSSION

Our results for the most part supported our predictions and revealed some new trends not reported before. For example, duration of flowering in annually flowering species, unlike episodically and supra-annual species, varied with the season or the time of flowering. Flowering duration within episodically flowering species was not negatively correlated with the number of episodes. Thus, the duration of flowering in episodically flowering species was an average of 3 wk longer during a year than that in annually flowering species. We next discuss variation in individual parameters, then relationships among parameters.

Variation in individual flowering characters—One of the earliest attempts to define flowering patterns was by Gentry (1974a, b), who classified the species of Bignoniaceae into five categories: steady state, modified steady state, cornucopia, big bang, and multiple bang. Flowering patterns also were compared based on alternative groupings of species, i.e., massive vs. extended (Bawa, 1983) or seasonal vs. extended (Frankie et al., 1974). Newstrom et al. (1994b) criticized these classification schemes not only because the meaning of these terms are somewhat different among authors, but also because these

TABLE 7. Two-way ANOVA of the effects of flowering time and phylogeny on flowering duration within classes of flowering frequency among tree species of the seven large families at La Selva, Costa Rica. Significance of factors was tested based on Type III sums of squares. An interaction term for supra-annually flowering species was not estimable because of limited sample size.

| Source of variation | Episodic | | | Annual | | | | Supra-annual | | |
|-----------------------|----------|------|----|--------|-------|-----|----------------|--------------|------|----|
| | df | F | P | df | F | P | R ² | df | F | P |
| Flowering time (Time) | 3 | 1.03 | ns | 3 | 10.84 | *** | 43.4 | 1 | 0.07 | ns |
| Phylogeny | 6 | 1.63 | ns | 6 | 1.04 | ns | | 4 | 0.15 | ns |
| Time × Phylogeny | 4 | 0.16 | ns | 7 | 0.54 | ns | | | | |
| Model | 13,28 | 1.22 | ns | 16,25 | 3.12 | ** | 66.7 | 5,4 | 0.12 | ns |

** $P < 0.01$; *** $P < 0.001$; ns = not significant.

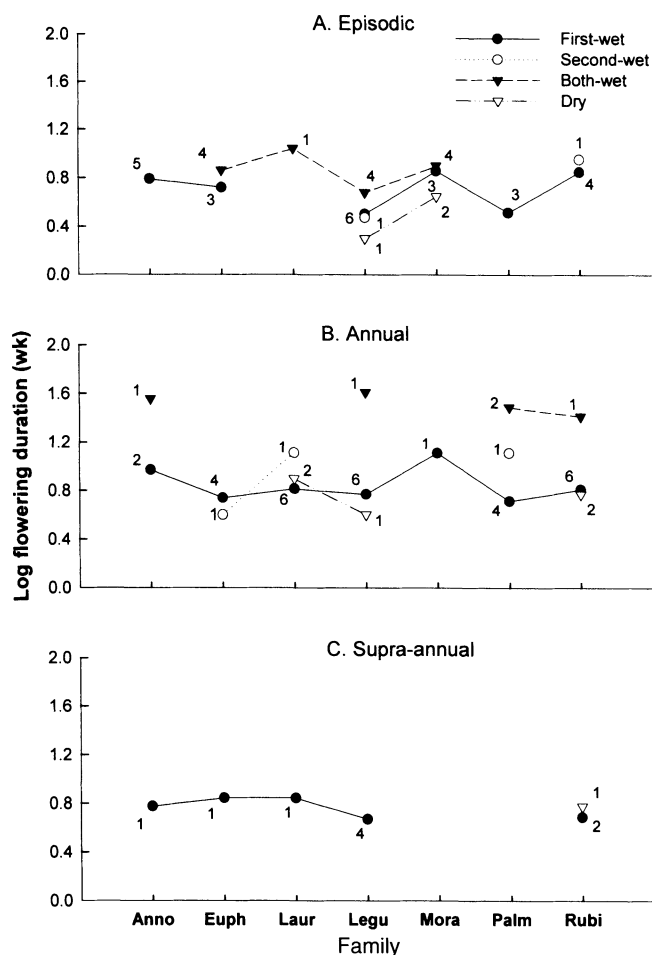


Fig. 8. Mean log of flowering duration of each of seven large families according to flowering time among episodically (A), annually (B), and supra-annually (C) flowering species. Numbers by symbols indicate the number of species of each family flowering in different seasons within each class of flowering frequency. Anno = Annonaceae; Euph = Euphorbiaceae; Laur = Lauraceae; Legu = Leguminosae; Mora = Moraceae; Palm = Palmae; Rubi = Rubiaceae.

terms connote several different aspects of flowering patterns. For example, "seasonal" implies brief flowering in either a wet or dry season while "massive" means brief flowering with high amplitude. "Extended" flowering also ranges from 2 wk or more (Opler et al., 1980) to 1 mo or more (Gentry, 1974a) to 5 mo or more (Frankie et al., 1974). Flowering time also has been represented by flowering season (Frankie et al., 1974; Opler et al., 1980; Bawa, 1983; Koptur et al., 1988; Bullock and Solís-Magallanes, 1990), midpoint of flowering (Kochmer and Handel, 1986), initiation and maximum flowering time (Smith-Ramírez and Armesto, 1994), overall flowering time (Wright and Calderon, 1995), and peak of flowering (Sakai et al., 1999). Because the proliferation of such terms has delayed our understanding of the evolution of flowering patterns, we defined clearer terms regarding flowering, such as flowering time (based on seasonality), frequency, and duration following Newstrom et al. (1994b).

Flowering time—Flowering timing or seasonality among La Selva species is relatively well known (e.g., Frankie et al., 1974; Opler et al., 1980; Newstrom et al., 1994a, b). Our re-

sults generally agree with previous ones. Our hypothesis of most species flowering in the season with the lowest rainfall was not supported by the data. Flowering activity peaks in July, the last month of the first wet season, and the lowest number of species flower in the second wet season with the highest rainfall. Most species in a tropical dry forest flower in the dry season because leaf fall in the dry season reduces water stress (Borchert, 1983) or because pollinators are most abundant in the dry season (Janzen, 1967). There are probably two reasons for a lack of peak flowering among trees in the dry season at La Selva. First, there is no pronounced dry season comparable to that in the dry tropical forest. Active leaf production in the dry season from February to April among La Selva species (Frankie et al., 1974) suggests that species in the wet tropical forest may not suffer from water stress during this dry season. Second, some pollinators, such as large beetles, sphinx moths, hummingbirds, and bats, are more abundant in the wet tropical forest than in the dry or cloud tropical forest (Frankie et al., 1983; Koptur et al., 1988; Bawa, 1990; Kress and Beach, 1994). Thus, species in the wet tropical forest are not under pressure to flower in the dry season to take advantage of vectors that might be abundant then.

Flowering frequency—We predicted that species that flower several times a year should be more common than species that flower annually, which in turn should be more abundant than species that flower supra-annually. In our data, annually flowering species are slightly more abundant than episodically flowering species (42% vs. 37%), and continually flowering species are less abundant than supra-annually flowering species (6% vs. 14%). Flowering intensity in continually flowering species may not be uniform and could consist of brief episodes of intense activity. Thus, when continually flowering species are included with episodically flowering species, our prediction of relative abundance of species flowering episodically is marginally supported. Interestingly, Newstrom et al. (1994b) reported that episodic flowering is more frequent than annual flowering (48% vs. 34%). The disparity may partly be due to year-to-year variation in flowering phenology among tropical species. Because the study by Newstrom et al. (1994b) was based on a longer period, we could have underestimated the proportion of episodically flowering species.

Although many plant species in the tropics display episodic flowering, little is known about its adaptive significance. The only detailed study of episodic flowering is that by Bullock et al. (1983). *Guarea rhopalocarpa* flowered five times a year, with 30–90% of trees flowering in each episode. Flowering lasted 1–6 wk per episode, with non-flowering intervals of up to 30 wk between episodes.

Multiple episodes may increase the number of mates and enhance reproductive success. Gentry (1974b) postulated that multiple clutches may have been selected to reduce reproductive failure from fluctuating populations of pollinators. Multiple broods of relatively small size may also reduce attractiveness to seed predators. Episodic flowering, however, may be constrained by fruit development and maturation and optimal timing for seed dispersal. If seeds and fruits mature over a long period of time, repeated flowering would not be possible. Similarly, if seed dispersal is seasonal, as is dispersal by wind during the dry season, there would be selection for annual flowering. Annual flowering probably also more effectively reduces the populations of seed predators between seed crops. Differences between annual and episodic flowering spe-

cies with respect to diversity and number of mates, fruit maturation time, seed dispersal, and seed predation should permit a test of these hypotheses.

That both continually and supra-annually flowering species are rare is not surprising. Continual flowering, which necessarily accompanies continual fruiting, requires special conditions to ensure resource acquisition. Indeed, these species tend to occur in patchy, sunlit habitats (Stiles, 1978; Opler et al., 1980) that are sparsely distributed. When continual flowering is treated as a variation of episodic flowering, supra-annually flowering species are least abundant as we predicted. Flowering once in several years is likely to confer a disadvantage because unpredictability of flowering will inhibit pollinator fidelity and specialization.

Flowering duration—Flowering duration can be defined at various levels such as individual flower, inflorescence, plant, population, and species (Primack, 1985). There are few quantitative analyses of variation in flowering duration, especially at the species level. In La Selva, species vary greatly in flowering duration from a few days to the entire year, though two-thirds of species are in flower for less than 2 mo. Yet variation in duration, as we predicted and as is discussed next, is linked with timing and frequency.

Relationship between flowering characters—**Relationship between flowering time and frequency**—We predicted that supra-annual species should flower during the dry season. Several authors have shown that supra-annual species flower massively mainly in the dry season (Frankie et al., 1974; Opler et al., 1980; Ashton et al., 1988). These species at La Selva have a higher probability of flowering in the dry season only when compared to episodically and annually flowering species. Contrary to our prediction, flowering of supra-annual species is not entirely restricted to the dry season. Seasonal transition according to rainfall often occurs during May at La Selva. Thus, we classified May as the first month of the first wet season. When we closely examine the flowering month of supra-annually flowering species, the number of flowering species increases steadily from February ($N = 3$) to a peak in June ($N = 11$). Combining flowering species across month, 17 of 29 supra-annually flowering species flower from February to May and 16 in June and July. Thus, whether or not a majority of supra-annually flowering species flower in the dry season depends upon the classification of the transitional month of May.

Supra-annual flowering may have evolved in response to selection to attract pollinators or to satiate seed predators (Janzen, 1974; Ashton et al., 1988; de Jong et al., 1992). Supra-annual flowering in a Bornean tropical forest has also been interpreted as a mechanism to increase mating opportunities by utilizing diverse general vectors (Sakai et al., 1999) and to reduce seed predation (Curran and Webb, 2000). Not enough is known about the supra-annually flowering species at La Selva to make inferences about underlying evolutionary forces.

Relationship between flowering time and duration—We predicted that species that bloom during the dry season or species in which flowering and vegetative growth are temporally separated should flower over a shorter period than species without such decoupling. Water level in the soil is often cited as a major factor affecting variation in flowering phenology of tropical forest species (Frankie et al., 1974; Opler et al., 1976;

Borchert, 1980, 1983; Bullock and Solís-Magallanes, 1990; but see van Schaik et al., 1993). One response to water stress is the temporal partitioning of vegetative growth and flowering activity. Using data pooled over species with different flowering frequencies, dry season flowering species flowered for a shorter period compared to those flowering in the wet season. However, the dry season itself may not impose short flowering. First, duration varies with season only among annually flowering species. Second, even among annually flowering species, species flowering in the first wet season are in bloom as briefly as those flowering in the dry season. Furthermore, duration of episodically and supra-annually flowering species is quite invariant regardless of season. The potential reasons for the interaction between flowering time, frequency, and duration are further described next.

Relationship between flowering frequency and duration—As predicted, both episodically and supra-annually flowering species flowered briefly compared to those flowering annually. However, the duration of flowering in annually flowering species, unlike episodically and supra-annually flowering species, is influenced by the time of flowering. For example, in species flowering annually in the first wet and dry season the duration was 4 and 6 wk less respectively than in those flowering in the second wet season. And species flowering annually in both-wet seasons flowered 2.6 to 6.6 times longer than those flowering in either wet or dry season. Variation in flowering duration among annually flowering species may be associated with the rate of flower production per day. On Barro Colorado Island in Panama, *Erythrina costaricensis* and *Pentagonia macrophylla* had a low population density and produced fewer flowers per day, but flowered over a longer duration than species flowering massively (Augsburger, 1983). Extended flowering in species that are restricted in space apparently increases mating opportunities over time. Continuous growth during the wet season may also provide resources for extended flowering.

In contrast to species that flower annually, flowering duration of episodically flowering species varies relatively little regardless of flowering time. Species flowering episodically bloom mostly 2–5 times per year but for a short period per episode, for example, for 2–3 d per episode in species of the Bignoniaceae (Gentry, 1974a, b) and the Melastomataceae (Bawa, 1983) and 1–6 wk in *Guarea rhopalocarpa* (Bullock et al., 1983). Because multiple flowering basically results in multiple fruiting, episodically flowering species may not be able to extend their flowering per flowering episode beyond a certain limit. Furthermore, these species flower repeatedly up to six times or more, and between-year variation in flowering time is large (Bullock et al., 1983; Bullock and Solís-Magallanes, 1990).

As predicted, supra-annual species flower for a brief period, i.e., less than 4 wk. Also, flowering duration of supra-annual species does not depend upon flowering time. Unpredictable flowering over time probably has selected massive display for a brief period to attract diverse pollinators. Massive flowering leaves little resources to maintain flowers for a long duration, regardless of flowering season.

The effect of phylogeny—Phylogeny has been shown to constrain flowering time in temperate plants (Kochmer and Handel, 1986; Johnson, 1992; Smith-Ramírez and Armesto, 1994). Such a constraint among confamilial species was not evident at La Selva. Our result also contradicts previous studies that

lacked quantitative analyses but showed that closely related species in the tropics tend to flower together in the same season (e.g., Frankie et al., 1974; Opler et al., 1980; Bullock and Solís-Magallanes, 1990). Recent analyses of species on Barro Colorado Island showed that different flowering characters are affected by phylogeny (Wright and Calderon, 1995). For example, congeners are similar with respect to overall flowering times, confamilials are similar for concentration of flowering time reflecting a temporal dispersion pattern of flowering across all months of a year, and monocots are similar in flowering midpoint, which is an intermediate time from the beginning to the ending of flowering. Thus, flowering phenology can be defined by various aspects of flowering, and the degree of divergence among related species needs to be separately examined for different aspects.

Flowering frequency in relation to phylogeny has not been examined before. Previous authors analyzed temperate zone species that, by-and-large, flower annually (Kochmer and Handel, 1986; Johnson, 1992; Smith-Ramírez and Armesto, 1994). For tropical species, Wright and Calderon (1995) excluded episodically flowering species from the data. Not only is flowering frequency a major character defining flowering patterns, but also 40–50% of La Selva species flower episodically. At La Selva, species of certain families flower with a certain flowering frequency, but not at a certain flowering time or for a particular duration.

Related species share the same or similar developmental pathways through a common descent. Flowering frequency might be a trait that is more strongly canalized than flowering time or duration. However, the number of episodes within a year is not particularly associated with phylogeny. Sub-annual flowering frequency of episodically flowering species varies greatly among years or between sexes among episodically flowering species (Bullock et al., 1983) and is believed to be a response to local rains (Bullock and Solís-Magallanes, 1990). Such environmental effects might contribute to the lack of phylogenetic effects on the number of episodes.

Flowering frequency and phylogeny could also be correlated because these two characters may be associated with an unexamined variable such as growth habit or successional status. This is not the case for the temperate rain forest plants of Chile where family membership, independently of habit, exerts strong effects on variation in duration and peak times of flowering among species (Smith-Ramírez and Armesto, 1994). We have examined the extent to which the phylogenetic effects on flowering frequency accrue through correlation with diverse ecological characters (Kang and Bawa, 2003).

Concluding remarks—We have shown that there is an association among flowering characters such as flowering time, duration, and frequency at La Selva. Moreover, evolution of frequency is constrained by phylogeny. Thus, inferences about selective pressures for the evolution of flowering traits in isolation of each other (and phylogeny) may not be valid. Other constraints, as we discuss in Kang and Bawa (2003), include successional status, habit, sexual system, and pollination system. To the best of our knowledge, no study has explored such constraints on the evolution of flowering, an important life cycle trait.

The second general point is that ecology and evolution of flowering phenology has largely been discussed in terms of timing of flowering and to a lesser extent duration (e.g., Janzen, 1967; Frankie et al., 1974; Gentry, 1974a, b; Stiles, 1978;

Opler et al., 1980; Koptur et al., 1988; Bullock and Solís-Magallanes, 1990). Frequency of flowering, particularly sub-annual flowering, has been largely ignored (but see Bullock et al., 1983; Newstrom et al., 1994a, b). Yet, we have shown, as have Newstrom et al. (1994), that approximately 50% of all tree species in the wet forest flower episodically. Episodic flowering may be the most common mode among tree species of wet tropical forests. Moreover, frequency is interrelated in a complex way with timing and duration. Thus, neither the timing nor the duration of flowering at the community level can be completely understood without taking into account the frequency of flowering. Documenting and understanding episodic flowering therefore is critical to understanding phenological patterns of many tropical plants as well as the evolution of flowering patterns at the community level.

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