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EFFECTS OF SUCCESSIONAL STATUS, HABIT, SEXUAL SYSTEMS, AND POLLINATORS ON FLOWERING PATTERNS IN TROPICAL RAIN FOREST TREES¹

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Based on data from observations of 302 tree species at La Selva, Costa Rica, we tested a range of hypotheses about the relationship between flowering parameters such as time, frequency, and duration and ecological features such as successional status, habit, sexual systems, and pollen vectors with and without considering the effect of family membership. We predicted that early successional species would flower any time of the year, but species pollinated by different vectors as well as dioecious species would flower nonrandomly across seasons. However, there was little evidence that flowering time varied with successional status, pollen vectors, and sexual systems. As we predicted, supra-annual flowering was proportionately less common in early successional species as compared to late ones, in understory species as compared to canopy species, and in dioecious species as compared to those with hermaphroditic flowers. When considering phylogeny, however, supra-annual flowering in the understory was not as rare as predicted. Our prediction of longer flowering in the early successional species as compared to late successional species was also supported. Predictions about longer flowering of dioecious species as compared to hermaphroditic species and of species pollinated by generalist vectors as compared to the specialists were not supported, though there was a trend in the expected direction.

Key words: Costa Rica; flowering patterns; phylogeny; pollinators; sexual selection; succession; tropical forests.

In another paper, we analyzed the relationships among flowering characters such as flowering time, frequency, and duration in tree species of a wet tropical rain forest and found that these three variables in flowering are associated with each other to generate complex flowering patterns (Bawa et al., 2003). Variables in flowering should also be strongly influenced by other reproductive characters such as pollen vectors and sexual systems that along with flowering time, frequency, and duration are selected to optimize reproductive success. Moreover, flowering patterns should also be influenced by successional status and habit, which themselves are correlated with sexual systems, pollination mechanism, and flower size (Darwin, 1877; Stebbins, 1970; Bawa, 1980a; Primack, 1987). However, there is no systematic treatment or discussion of how timing, frequency, and duration of flowering may be influenced by pollination mechanism, sexual systems, habit, or successional status. Here, using data for 302 species from the tropical wet evergreen forest at La Selva, Costa Rica, we examine how time, frequency, and duration of flowering correlate with sexual systems, pollination mode, successional status, and growth habit. We first propose hypotheses about the relationships between each major variable of flowering and other reproductive traits as well as growth habit and successional status. We then test predictions of these hypotheses with data from the wet, evergreen forest plants. The results not only conform to predictions, but also reveal new relationships not reported before.

Flowering time—Based on hypotheses that early successional species are *r*-selected and have evolved to rapidly use

transient habitats (Baker, 1974; Bazzaz, 1979; Bazzaz and Pickett, 1980), these species should be selected to flower and fruit any time of the year, unless constrained by pollinators or seed dispersal agents. Species pollinated by different vectors, on the other hand, should have evolved to flower at a time when these pollinators are most abundant. For example, in the dry forest, pollinating moths are abundant in the wet season (Haber and Frankie, 1989), medium-sized bees in the dry season (Janzen, 1967). Although the dry season in the wet, evergreen forests is not as pronounced as in the dry forest, flowering of species pollinated by different vectors may be seasonal, though not to the same extent as in the dry forest. Because there is an association between dioecy and generalist insects as pollen vectors (Bawa, 1980b), flowering of dioecious species may also be seasonal.

In summary, in relation to timing we predict that early successional species should flower any time of the year, but species pollinated by various pollen vectors as well as dioecious species should flower nonrandomly across seasons.

Flowering frequency—In colonizing species, selection for rapid growth, early reproductive maturity, and relatively high reproductive effort (Baker, 1974; Bazzaz, 1979; Bazzaz and Pickett, 1980) should make the evolution of supra-annual flowering unlikely. Supra-annual flowering is made possible through stored reserves (Bullock and Solís-Magallanes, 1990; Oyama and Mendoza, 1990; Bullock, 1992). Such species flower massively over brief periods (Ashton et al., 1988; de Jong et al., 1992; Appanah, 1993) to recruit pollinators. Understory species are less likely to accumulate reserves and should not be selected to have massive displays that function especially well for canopy species where long-distance visual cues may be important for pollinators. Thus, supra-annual flowering should be less common in understory than in canopy species. Finally, dioecious species should be selected to have an extended flowering period as will be argued later. By in-

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ference, supra-annual flowering should be rare among dioecious species.

Briefly then, supra-annual flowering should be less common in early successional as compared to late successional species, understory as compared to canopy species, and dioecious as compared to hermaphroditic species.

Flowering duration—Because early successional species have greater access to such resources as sunlight and nutrients (Percy, 1983; Vitousek and Denslow, 1986; Becker et al., 1988), these species should flower over a longer period than late successional species. Understory species, too, should exhibit extended flowering, because they may not accumulate enough reserves, as mentioned earlier, for short episodes of massive blooming. Massive blooming might also be selected against because the *raison d'être* for massive blooming is the ability of such flowering to visually attract pollinators from long distances.

In dioecious species, a division of labor is associated with sexual reproduction (Darwin, 1877). Individuals thus should have more resources for flowering and fruiting than do hermaphroditic species. Intra-sexual selection among males should also be more intense than for hermaphrodites because the males in dioecious species do not have to bear the cost of seed production. Competition among males may also select for longer breeding seasons. Indeed males flower for a longer period than the females in dioecious species (Bawa, 1980b; Bullock et al., 1983). Thus, on the basis of energetics and sexual selection, dioecious species should flower for a longer period than hermaphroditic species.

Reliability of pollination should also influence duration of flowering. Specialization in mutualistic interactions is assumed to result in reliability and predictability of benefits conferred by mutualists on each other, whereas generalist interactions may have the opposite effects (Waser et al., 1996; Wilson and Thompson, 1996; Johnson and Steiner, 2000).

Thus, flowering duration should be longer in early successional as compared to late successional species, understory species as compared to canopy species, dioecious species as compared to hermaphroditic species, and species pollinated by generalist vectors as compared to specialized vectors.

We first describe the distribution of ecological characters such as successional status, habit, sexual systems, and pollen vectors among La Selva tree species. We then focus on the association between flowering and ecological characters. The relationship between flowering and ecological characters could be confounded by a taxonomic membership of species if certain speciose taxa possessed a particular ecological character(s). Thus, we reexamine the relationship between flowering and ecological characters after excluding the effect of phylogeny acting at the level of family.

MATERIALS AND METHODS

This study was conducted over 3 yr (1978–1980) at the La Selva Biological Station of the Organization for Tropical Studies in Costa Rica. The Biological Station located in the province of Heredia, Costa Rica (10°20' N, 83°59' W), is a typical tropical wet forest with an annual rainfall of 4000 mm. Because species diversity is extremely high, population density is quite low, less than one individual (dbh > 10 cm) for 70% of the tree and liana species (Clark, 1994). More than 1000 individuals belonging to 302 species of 58 families were marked along the trails of the station. Sample size per species ranged from one to many (see Bawa et al., 2003). Flowering time, frequency, and duration per flowering episode were observed weekly for tree species.

Because many species flowered in different months during the 3 yr of observations, flowering months were obtained by pooling the 3 yr of data for each species. Flowering time was then classified into four levels (first-wet, second-wet, both-wet, and dry), which were primarily distinguished by flowering in the first (May–July) or second (November–January) wet season, or the dry season (see Bawa et al., 2003 for description).

Flowering frequency was classified into four levels based on flowering frequency per year (annual flowering frequency): continual species that flower more or less continually throughout a year, episodic species that flower twice or more times a year, annual species that flower once a year, and supra-annual species that do not flower every year. For most episodically flowering species, the minimum flowering frequency per year (sub-annual flowering frequency) was also ascertained. The sub-annual flowering frequency is categorized into three levels (twice, three, and four or more times). Flowering duration per episode was treated as a continuous variable, ranging from less than 1 wk to up to 40 wk. Throughout this paper, if not specifically mentioned, flowering duration represents the duration per episode. For detailed descriptions for these flowering characters see Bawa et al. (2003).

Ecological information such as successional status and habit was obtained *in situ*. Data on sexual systems and pollen vectors were collected from previous studies (Bawa et al., 1985a,b; Kress and Beach, 1994) at the same site. The successional status and habit of each tree species were classified into two categories, respectively, early vs. late successional status and understory vs. canopy species. Because the number of emergent species was few ($N = 6$), these species were combined with canopy species. Three sexual systems were distinguished, *i.e.*, species with hermaphroditic flowers, monoecious flowers, and dioecious flowers. Thirteen different categories of pollen vectors were identified based on Bawa et al. (1985a) and Kress and Beach (1994). Depending upon analyses, the pollen vector consists of five categories (the five most common vectors such as small bees, medium/large bees, beetles, moths, and small insects) or two categories (specialists including medium/large bees, beetles, hawk moths, bats, and hummingbirds and generalists including small bees, moths, small diverse insects, butterflies, wasps, thrips, wind, and flies).

We first examined the association between pairs of ecological and categorical flowering characters (flowering time and frequency). The association between these categorical characters was examined in two-way contingency table analyses on data pooled over all 58 families. The relationship between ecological characters and flowering duration was examined using ANOVAs with flowering duration as a dependent variable since flowering duration was treated as a continuous variable. We also examined the associations of phylogeny with ecological characters. Seven large families comprising 47.4% of the total 302 species were used as classes of the phylogeny variable in two-way contingency tables of phylogeny by each ecological character. In these contingency table analyses, we identified the categories that contributed significantly to the G value based on the adjusted standardized residuals. Because of limited sample size, the association between categorical variables could not be tested independently of phylogeny using a three-way table such as successional status \times flowering time \times phylogeny. Thus, the relationship between categorical characters after considering phylogeny was examined based on a subset data of species of 43 minor families with ≤ 5 species each (number of species per family = 2.37 ± 1.24 , mean ± 1 SE, $N = 102$). On the other hand, the relationships between ecological characters and flowering duration after considering phylogeny were directly tested with ANOVA incorporating phylogeny as a class variable. Only successional status among ecological characters was consistently associated with flowering frequency and duration. Thus, the relationship between flowering time, frequency, phylogeny, successional status, and duration was simultaneously examined in ANOVA with flowering duration as a dependent variable. Because of small and unbalanced sample sizes, only two-way interactions were considered in this ANOVA. When the effects of factors involving successional status were examined separately for each flowering frequency category, only episodic and annual flowering were considered since supra-annual flowering was found in only late successional species.

Data on ecological as well as on flowering characters of each species were not entirely complete. For example, the successional status was recorded for all of the species listed, but the type of pollen vector was known for about

TABLE 1. Successional status, habit, sexual system, and pollen vector of tree species (58 families) at La Selva, Costa Rica. Because more than one type of pollen vector visits flowers in some species (total $N = 145$ species), the cumulative percentage of species visited by pollen vectors is over 100%.

Ecological character	<i>N</i>	%
Successional status		
Early	63	20.9
Late	239	79.1
Habit		
Understory	225	74.5
Canopy	77	25.5
Sexual system		
Hermaphroditic flowers	186	63.3
Monoecious flowers	40	13.6
Dioecious flowers	68	23.1
Pollen vector		
Small bee	27	18.6
Medium/large bee	42	29.0
Beetle	13	9.0
Moth	11	7.6
Small insect	26	17.9
Hummingbird	8	5.5
Butterfly	8	5.5
Hawk moth	6	4.1
Bat	6	4.1
Wind	5	3.4
Wasp	3	2.1
Fly	3	2.1
Thrip	1	0.7

only half the number of species. Therefore, several two-way contingency tables, especially those involving the pollen vectors or phylogeny, created cells with low or zero count, violating the assumption of less than 20% of the cells with expected counts < 5 (Marascuilo and Levin, 1983). Contingency table analyses were still conducted to obtain a preliminary idea for the relationship between ecological and flowering characters. Flowering duration per episode was log transformed (base 10). The species flowering continually ($N = 15$) with no variation in flowering duration were deleted when conducting analyses of variance. Means of flowering duration are given with 1 SD throughout this paper. All analyses were conducted using the SAS (1999) 8.1 package.

RESULTS

Description of ecological characters—Late successional species were about four times more numerous than early successional species among La Selva tree species (Table 1). Three quarters of species examined were understory species. Species with hermaphroditic flowers had the highest proportion (63.3%), followed by dioecious (23.1%) and monoecious species (13.6%). For tree species with only one type of vector identified, medium/large-sized bees were the most frequent vector (29.0%).

Relationship between ecological characters and phylogeny—All ecological characters were significantly associated with phylogeny (Table 2). A disproportionate segregation of confamilial species was particularly notable for sexual system. Thus, among the seven large families, three families were characterized by a single sexual system (hermaphroditic flowers), another three predominantly by one sexual system, and only a single family by two sexual systems, both with unisexual flowers.

Similarly, certain families were associated with a single type of pollen vector, for example, the Annonaceae with beetles and the Euphorbiaceae with small insects. The Moraceae had two

TABLE 2. Frequency of La Selva tree species in seven large families across levels of ecological variables. Likelihood ratio chi square (G) is reported for each two-way contingency table.

Ecological character	Families						
	Anno	Euph	Laur	Legu	Mora	Palm	Rubi
Successional status							
Early	0	6	3	3	4	1	9
Late	13	13	11	27	13	20	20
	$G = 15.34^*$						
Habit							
Understory	11	15	9	16	12	20	26
Canopy	2	4	5	14+	5	1	3
	$G = 18.52^{**}$						
Sexual system							
Hermaphroditic	13	0-	14+	30+	0-	0-	27+
Monoecious	0	10+	0	0-	2	20+	0-
Dioecious	0	8+	0	0-	15+	1	2
	$G = 212.21^{***}$						
Pollen vector							
Small bee	0	0	0	2	0	6	4
Medium/large bee	0	0	0	11+	0	2	3
Beetle	6+	0	1	0	0	5	0
Moth	0	0	0	2	0	0	0
Small insect	0	5+	0	0	0	1	0
	$G = 73.33^{***}$						

Note: Anno = Annonaceae; Euph = Euphorbiaceae; Laur = Lauraceae; Legu = Leguminosae; Mora = Moraceae; Palm = Palmae; Rubi = Rubiaceae. A +/- sign indicates observed values were greater or less than the expected value at alpha = 0.05 level.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 3. Frequency of La Selva tree species in two-way contingency tables of combination pairs of flowering time and ecological variables. Likelihood ratio chi square (G) is reported for each two-way contingency table. Analyses were conducted twice based on data set A, including species of all families, and data set B, including species of 43 minor families.

Ecological character	Flowering time							
	A				B			
	First-wet	Second-wet	Both-wet	Dry	First-wet	Second-wet	Both-wet	Dry
Successional status								
Early	27	5	19	11	8	2	5	6
Late	129	24	43	36	39	14	10	14
	$G = 4.92$ ns				$G = 3.37$ ns			
Habit								
Understory	110	20	51	39	30	11	11	16
Canopy	46	9	11	8	17	5	4	4
	$G = 5.76$ ns				$G = 1.93$ ns			
Sexual system								
Hermaphroditic	96	18	34	32	28	8	9	12
Monococious	24	2	11	3	3	1	2	1
Dioecious	31	7	17	11	15	5	4	6
	$G = 6.33$ ns				$G = 1.01$ ns			
Pollen vector								
Small bee	12	2	5	2	4	1	1	0
Medium/large bee	21	4	7	4	7	3	1	2
Beetle	10	0	2	1	1	0	0	0
Moth	3	3	3	0	0	2	0	0
Small insect	14	3	6	2	8	2	2	3
	$G = 10.29$ ns				$G = 10.60$ ns			

ns = not significant.

species with wasps as pollen vectors and three with wind. Both generalist and specialist vectors were well represented only in the Leguminosae, Palmae, and Rubiaceae among the seven large families. However, Leguminosae was strongly associated with medium/large bees, while Palmae and Rubiaceae were associated with a range of pollen vectors such as small bees, medium/large bees, beetles, moths, butterflies, and hummingbirds. Thus, family membership of La Selva tree species might confound the relationship between flowering parameters and ecological characters.

Relationship between flowering and ecological characters—*Flowering time and individual ecological characters*—THE PATTERN BEFORE CONSIDERING PHYLOGENY—Early successional species flowered across all flowering seasons with peak flowering in the first-wet season and the lowest number of species flowering in the second-wet season. However, early and late successional species did not differ in the relative proportion of flowering species across seasons (Table 3A).

The two-way interactions of flowering time with the five most common vectors (Table 3A) and with specialist vs. generalist vectors ($G = 1.34$, $P \gg 0.05$, $df = 3$, N [total] = 138) were not significant. Thus, the seasonal pattern of the number of flowering species did not differ among species pollinated by the five most common vectors or by specialist and generalist vectors. Even when the monthly pattern of flowering species visited by these two groups of vectors within the Leguminosae, Palmae, and Rubiaceae was examined, generalist vectors were quite rare throughout the year (Leguminosae and Rubiaceae) or as seasonal as specialist vectors (Palmae) (Fig. 1). Thus, generalist vectors are not more active during certain months compared to specialist vectors. When all vectors were included, there appeared to be some pattern that was dependent upon the vectors. For example, three of the four hawk

moth-visited species flowered in the first-wet season, and their flowering occurred only from April to June. Bat- and hummingbird-visited species tended to have a distinct pattern of seasonal flowering. Bat-visited species such as *Ceiba pentandra* and *Quararibea parvifolia* (both the Bombacaceae) flowered in the second-wet season; none of the four bat-visited species flowered in the first-wet season. Hummingbird-visited species flowered in the both-wet season (*Symphonia globulifera* [Guttiferae], *Psychotria elata*, *P. poeppigiana*, and *Hamelia patens* [call the Rubiaceae]) or in the first-wet season (*Erythrina cochleata* [Leguminosae] and *Pentagonia donnell-smithii* [Rubiaceae]) and none in the second-wet season. However, more than one species was visited by these two specialized vectors in any month of the year because a large proportion of wet-season flowering species, e.g., 78% of the first-wet season flowering species, also bloom during the dry season.

In addition, dioecious species did not have a higher probability of flowering at a certain season than species with hermaphroditic flowers (Table 3A).

THE PATTERN AFTER CONSIDERING PHYLOGENY—Species of 43 minor families did not show different patterns of association between flowering time and ecological characters from species of all families (Table 3B).

Flowering frequency and individual ecological characters—THE PATTERN BEFORE CONSIDERING PHYLOGENY—There was significant interaction between flowering frequency and several ecological characters such as successional status, habit, and sexual system (Table 4A). Species flowering continually and those flowering once in several years contributed largely to this interaction. Episodically and annually flowering species did not appear to be distinguished by a particular successional status, growth habit, and sexual system.

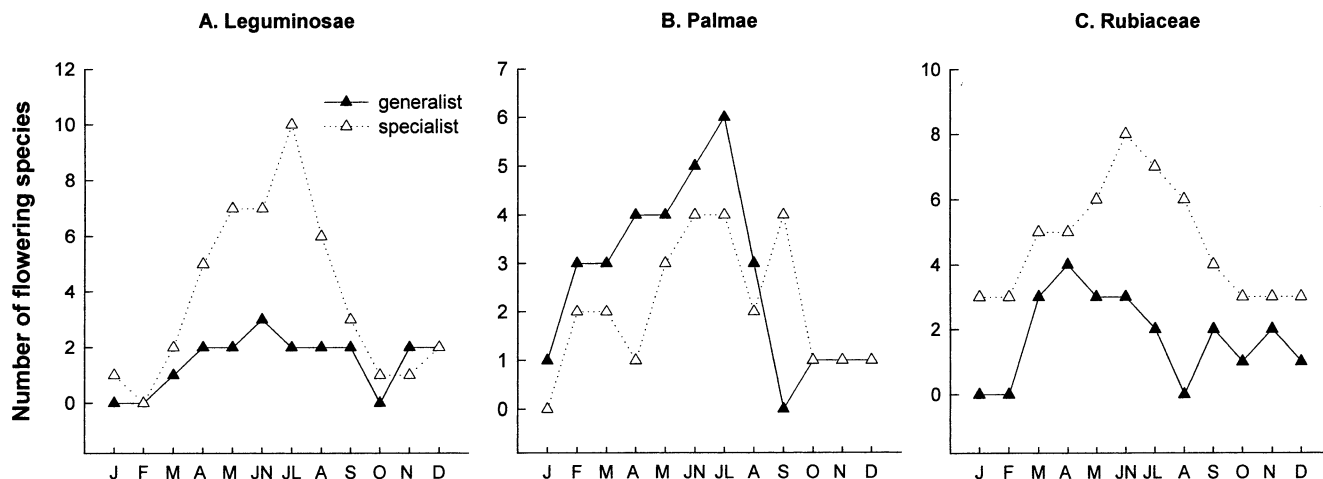


Fig. 1. Proportion of generalist vs. specialist vectors visiting species of Leguminosae, Palmae, and Rubiaceae during each month of a year at La Selva, Costa Rica.

Supra-annual flowering in late successional status was 16 times higher than that in early successional status. Conversely, continual flowering was proportionately more common in early successional than in late successional taxa. Only about half of the supra-annually flowering species existed in the understory, while 100% of continually flowering species occurred in the understory. Flowering frequency was significantly associated with sexual system (Table 4A). Although no categories contributed significantly to the *G* score, the probability of finding species with hermaphroditic flowers was, in species flowering supra-annually, nine times higher than that of dioecious species.

The relationship between flowering frequency and the five most common pollen vectors was statistically insignificant (Table 4A). However, the data indicated some, but not simple, associations between flowering frequency and pollen vectors. For example, only medium/large bees and small insects were recorded across all levels of flowering frequency. Small bees and wind were entirely associated with episodically or annually flowering species. Contrast also existed between bat- and hummingbird-visited species. The bat-visited *Quararibea parvifolia* (Bombacaceae) and one *Calyptronyne* species (Palmae) flowered episodically, and *Ceiba pentandra* (Bombacaceae) flowered supra-annually. None of the bat-visited species

TABLE 4. Frequency of La Selva tree species in two-way contingency tables of combination pairs of flowering frequency and ecological variables. Likelihood ratio chi square (*G*) is reported for each two-way contingency table. Analyses were conducted twice based on data set A, including species of all families, and data set B, including species of 43 minor families.

Ecological character	Flowering frequency							
	A				B			
	Continual	Episodic	Annual	Supra-annual	Continual	Episodic	Annual	Supra-annual
Successional status								
Early	8+	16	23	2	1	5	11	0
Late	7	74	79	32	2	20	29	15
	<i>G</i> = 14.33***				<i>G</i> = 8.27*			
Habit								
Understory	15	68	72	18	3	18	24	10
Canopy	0–	22	30	16+	0	7	16	5
	<i>G</i> = 16.07***				<i>G</i> = 3.53 ns			
Sexual system								
Hermaphroditic	12	50	61	28	3	14	21	12
Monoecious	1	14	14	1	0	3	2	1
Dioecious	2	24	26	3	0	7	16	2
	<i>G</i> = 13.61*				<i>G</i> = 8.21 ns			
Pollen vector								
Small bee	0	7	10	0	0	3	3	0
Medium/large bee	2	10	16	5	0	4	8	1
Beetle	1	5	6	0	0	0	1	0
Moth	0	5	3	1	0	0	2	0
Small insect	1	7	14	1	0	3	9	1
	<i>G</i> = 12.45 ns				<i>G</i> = 4.62 ns			

Note: A +/- sign indicates observed values were greater or less than the expected value at alpha = 0.05 level.
 * *P* < 0.05; *** *P* < 0.001; ns = not significant.

bloomed continually. Three out of six hummingbird-visited species such as *Psychotria elata*, *C. poeppigiana*, and *Hamelia patens* were continually flowering species of the Rubiaceae, whereas this specialized vector visited none of the supra-annually flowering species.

The sub-annual flowering frequency of episodically flowering species was not particularly associated with any ecological character (two-way contingency table of sub-annual flowering frequency with successional status, $G = 1.94$, $df = 2$; with habit, $G = 2.78$, $df = 2$; with sexual system, $G = 3.04$, $df = 4$; with pollen vector, $G = 10.87$, $df = 8$, $P > 0.05$ for all analyses, $N[\text{total}] = 72, 72, 70$, and 28 , respectively).

THE PATTERN AFTER CONSIDERING PHYLOGENY—Among species of minor families, only the association between flowering frequency and successional status remained significant (Table 4B); the absence of supra-annually flowering species in the early successional status was notable. Supra-annual flowering in understory species was not rare among species of the minor families (Table 4B), suggesting that the association of supra-annual flowering and canopy was largely accrued through the effect of phylogeny. The G score for the association of flowering frequency and sexual system was substantial: among supra-annually flowering species of the minor families, species with hermaphroditic flowers were six times more frequent than those with dioecious flowers.

Flowering duration and individual ecological characters—**THE PATTERN BEFORE CONSIDERING PHYLOGENY**—Only the effect of the successional status on flowering duration was significant among ecological characters examined, accounting for only 8.9% of the total variance (Table 5). Early successional species flowered twice as long as late successional species.

Canopy and understory species did not differ in mean flowering duration (Table 5). Mean flowering duration of early and late successional species differed significantly even when only the understory species were considered ($F_{1,140} = 19.94$, $P < 0.001$).

Dioecious species flowered 1 to 2 wk longer than the monoecious and hermaphroditic species, but the effect of sexual system was not significant (Table 5).

Species pollinated by 12 different vectors differed by five-fold in mean flowering duration. Mean duration increased in the order of bat < wind < hawk moth, thrip < medium/large bee, beetle, wasp, moth < butterfly < small insect, small bee < hummingbird (Table 5). However, the effect of pollen vectors on flowering duration was statistically insignificant among all 12 vectors as well as between generalist vs. specialist vectors (Table 5). Notably, species visited by the two vertebrate vectors differed markedly in flowering duration. For example, bat-pollinated *Ceiba pentandra* flowered supra-annually for 3 wk and *Quararibea parvifolia* flowered episodically for less than 1 wk. Hummingbird-pollinated species bloomed for many weeks, for example, *Symphonia globulifera* (Guttiferae) for 8 wk per episode, *Pentagonia donnell-smithii* (Rubiaceae) for more than 20 wk, and *Psychotria elata*, *P. poeppigiana*, and *Hamelia patens* (all the Rubiaceae) continually throughout a year.

To avoid the confounding effect of flowering frequency on flowering duration, the relationship between flowering duration and successional status, habit, sexual systems, and pollen vectors was examined separately for each flowering frequency

TABLE 5. Means and standard deviations of flowering duration per episodes (in weeks) for each level of ecological characters among tree species at La Selva, Costa Rica. Analyses were based on data including species pooled over all families. A shared letter within each class variable indicates differences between means were not significant at alpha = 0.05 level. Multiple range test for pollen vectors was applied to only the means of species visited by generalist and specialist vectors.

Ecological character	X	SD	N
Successional status			
Early	9.39 ^A	1.92	34
Late	5.00 ^B	1.94	170
$F_{1,202} = 19.66$ ***, $R^2 = 8.9\%$			
Habit			
Understory	5.58 ^A	2.07	142
Canopy	5.56 ^A	1.81	62
$F_{1,202} = 0.00$ ns			
Sexual system			
Hermaphroditic	5.19 ^A	1.99	124
Monoecious	5.87 ^A	1.99	27
Dioecious	6.78 ^A	1.97	48
$F_{2,196} = 1.96$ ns			
Pollen vector			
Small bee	7.88	2.02	15
Medium/large bee	5.73	2.13	29
Beetle	5.88	2.19	11
Moth	6.12	2.39	8
Small insect	7.72	1.82	20
Hummingbird	12.75	1.82	2
Butterfly	7.49	1.09	2
Hawk moth	4.82	3.07	5
Bat	2.63	1.74	3
Wind	4.09	1.98	3
Wasp	6.00	—	1
Thrip	5.00	—	1
$F_{11,86} = 0.74$ ns			
Generalist	7.11 ^A	1.93	50
Specialist	5.62 ^A	2.20	50
$F_{1,98} = 1.96$ ns			

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

category. The longer flowering duration of early successional species relative to late successional was significant only in species flowering episodically, though this trend was also noticed in species flowering annually (Table 6, Fig. 2). Dioecious species as compared to those with hermaphroditic flowers—and species visited by generalist vectors as compared to specialist vectors—tended to flower longer, though statistically not significantly across flowering frequency categories (Table 6, Fig. 2). Understory and canopy species did not differ in mean flowering duration regardless of flowering frequency.

Since episodic species flower multiple times a year, the effect of ecological characters on flowering duration per year was also examined in species flowering episodically. For example, episodically flowering species in early successional status flowered 2.3 times longer during a year than late successional species ($F_{1,68} = 12.79$, $P < 0.001$; early successional, $X = 21.62 \pm 1.72$ wk, $N = 13$; late successional, $X = 9.46 \pm 2.08$ wk, $N = 57$). Also, on a yearly basis, monoecious and dioecious species tended to flower 3–6 wk longer than the hermaphroditic species ($F_{2,65} = 2.75$, $P = 0.071$; hermaphrodite, $X = 9.04 \pm 2.23$ wk, $N = 37$; monoecy, $X = 12.34 \pm 2.31$ wk, $N = 11$; dioecy, $X = 15.03 \pm 1.66$ wk, $N = 20$). However, yearly flowering duration did not differ either be-

TABLE 6. One-way ANOVA of the effects of successional status, habit, sexual system, and vector on variation in flowering duration for each category of flowering frequency among tree species at La Selva, Costa Rica. Because supra-annually flowering species are all late successional species, the effect of successional status was not tested for supra-annually flowering species.

Source of variation	Episodic				Annual				Supra-annual		
	df	F	P	R ²	df	F	P	R ²	df	F	P
Successional status	1,79	13.33	***	14.4	1,88	3.10	(*)	3.4	1,21	0.29	ns
Habit	1,79	0.13	ns		1,88	0.01	ns		2,18	0.46	ns
Sexual system	2,76	2.05	ns		2,86	0.68	ns		1,7	0.76	ns
Vector ^a	1,37	1.19	ns		1,47	1.07	ns				

^a Vector = pollen vector (generalist vs. specialist).
 (*) $P = 0.0819$; *** $P < 0.001$; ns = not significant.

tween species with different habits or between species visited by different vectors ($F_{1,68} = 0.22$ and $F_{1,33} = 1.61$, respectively, $P \gg 0.05$ for both).

THE PATTERN AFTER CONSIDERING PHYLOGENY—In all ANOVAs with phylogeny and one of the ecological characters as main factors, neither two-way interaction terms nor phylogeny had significant effects (Table 7). Only successional status among ecological characters had a significant effect on flowering duration: early successional species exhibited 1.6 times

longer flowering than late successional species ($X = 9.48 \pm 2.41$ wk and 5.87 ± 1.84 wk, $N = 13$ and 56 , respectively). Thus, the relationship between ecological characters and flowering duration did not change after considering phylogeny.

Flowering duration and pairs of ecological characters—In the two-way models of successional status with habit, with sexual system, and with pollen vectors, only successional status exerted a significant effect on flowering duration (Table 8). The effect of successional status differed with pollen vectors,

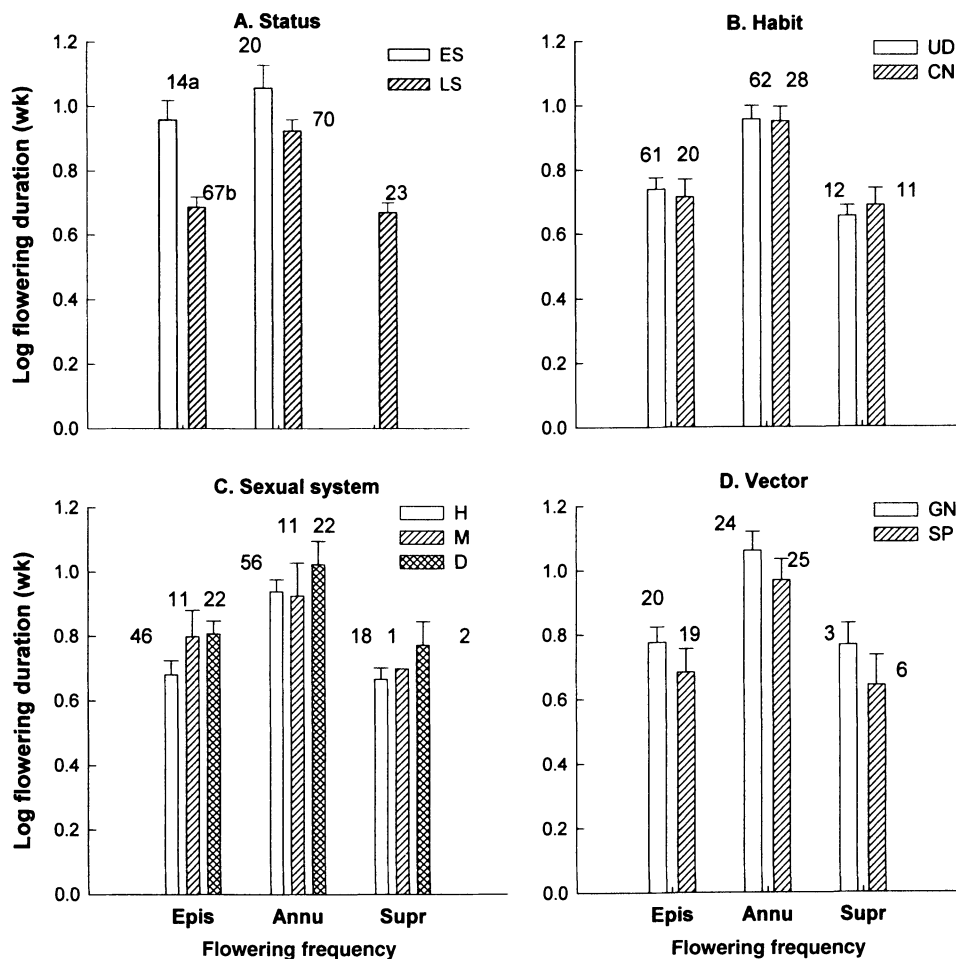


Fig. 2. Log flowering duration for each class of flowering frequency (Epis = episodic; Annu = annual; Supr = supra-annual flowering) according to (A) successional status (early [ES] vs. late [LS] successional), (B) habit (understory [UD] vs. canopy [CN]), (C) sexual system (hermaphroditic [H] vs. monoecious [M] vs. dioecious [D] flowers), and (D) pollen vector (generalist [GN] vs. specialist [SP]) (means + 1 SE). Numbers near bars represent the number of species in different categories of ecological characters within flowering frequency categories, and different letters after numbers represent significant differences in flowering duration between levels of ecological characters within each flowering frequency.

TABLE 7. Two-way ANOVA of the effects of phylogeny and one of the ecological characters on flowering duration per episode among tree species at La Selva, Costa Rica. Tests for significance of factors were based on the Type III sums of squares.

Class variable A × B	Overall model				A factor			B factor			A × B interaction		
	df	F	P	R ²	df	F	P	df	F	P	df	F	P
Phylogeny × Status	11,90	2.69	**	24.8	6	0.91	ns	1	14.75	***	4	1.42	ns
Phylogeny × Habit	13,88	1.18	ns		6	1.49	ns	1	0.36	ns	6	1.15	ns
Phylogeny × Sex	9,91	1.39	ns		6	1.77	ns	2	1.11	ns	1	0.35	ns
Phylogeny × Vector	10,39	0.64	ns		6	0.85	ns	1	0.13	ns	3	0.24	ns

Note: Status = successional status; Vector = pollen vector (generalist vs. specialist).
** $P < 0.01$; *** $P < 0.001$; ns = not significant.

but only marginally ($P = 0.0428$). For example, among species visited by specialist vectors, early successional species flowered four-fold longer than late successional species ($F_{1,48} = 11.35$, $P < 0.01$); among species visited by generalist vectors, the former flowered 1.5-fold longer than the latter ($F_{1,45} = 2.18$, $P = 0.1471$). This interaction is most likely because three of the four early successional species visited by specialist vectors (*Jacaratia dolichaula*, *Hamelia xerocarpa*, and one *Senna* species) flower for an extremely long period, for example, from 25 to 40 wk. Thus, the effect of successional status on flowering duration may be largely independent of the other ecological characters.

Relationship between flowering time, frequency, phylogeny, successional status, and flowering duration—The relationship between successional status and flowering duration was further examined by incorporating flowering time, frequency, and phylogeny (of seven large families) because these variables were correlated with each other. In a four-way ANOVA with flowering time, frequency, phylogeny, and successional status as main factors, flowering duration varied significantly with successional status, but marginally significantly with flowering time (Table 9). The two-way interaction effect of flowering frequency × successional status was marginal ($P = 0.1555$). Thus, three-way ANOVAs with flowering time, frequency, and phylogeny were separately conducted for species flowering episodically and annually. In species flowering episodically, only the effect of successional status was significant (Table 10), and early successional species flowered 2.8 times longer than late successional species (Fig. 3). However, in species flowering annually, flowering duration varied significantly only with flowering time (Table 10), though there was a trend toward longer flowering in early successional species than in late successional species (Fig. 3). Phylogeny was not an important factor contributing to variation in flowering duration despite

its correlation with flowering frequency and successional status.

Summary of results—(1) Early successional species flowered in all seasons, with peak flowering in the first-wet and the least flowering in the second-wet season. The seasonal pattern of flowering in early successional species did not differ from that in late successional species. Flowering time did not segregate differentially depending upon sexual system and pollen vector. (2) Supra-annual flowering was proportionately less common in early successional species as compared to late successional, understory species compared to canopy, and, probably, in dioecious species compared to hermaphroditic. (3) Flowering duration was longer in early successional than in late successional species and tended to be longer in dioecious species as compared to hermaphroditic and in species visited by generalist vectors rather than specialists. However, flowering duration did not differ between understory and canopy species. (4) Confamilial species of the seven large families were characterized by distinct ecological characters. Thus, after considering phylogeny, supra-annual flowering was still relatively rare in early successional species and tended to be so in dioecious species, but not in understory species. The associations between ecological characters and flowering duration did not change after considering phylogeny. However, the associations were not concordant among species characterized by different flowering frequencies. Overall, among ecological characters examined, successional status was the single significant factor associated with flowering frequency and flowering duration independently of phylogeny and other ecological characters.

DISCUSSION

Results in general conform to our predictions, but a few of our predictions did not hold. At the same time, our analyses

TABLE 8. Two-way ANOVA of the effects of pairs of ecological characters on flowering duration per episode among tree species at La Selva, Costa Rica. Tests for significance between factors were based on the Type III sums of squares. The interaction between successional status and habit could not be estimated because canopy species were absent in early successional status.

Class variable A × B	Overall model				A factor			B factor			A × B interaction		
	df	F	P	R ²	df	F	P	df	F	P	df	F	P
Status × Habit	2,201	10.76	***	9.7	1	21.51	***	1	1.78	ns			
Status × Sex	5,193	4.72	***	10.9	1	8.88	**	2	0.47	ns	2	1.90	ns
Status × Vector	3,93	5.69	**	15.5	1	13.54	***	1	0.73	ns	1	4.22	*
Habit × Sex	5,193	0.85	ns		1	0.11	ns	2	1.56	ns	2	0.20	ns
Habit × Vector	3,93	0.84	ns		1	0.07	ns	1	2.41	ns	1	0.08	ns
Sex × Vector	5,90	1.04	ns		2	0.50	ns	1	0.01	ns	2	1.30	ns

Note: Status = successional status; Sex = sexual system; Vector = pollen vector (generalist vs. specialist).
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant.

TABLE 9. Four-way ANOVA of the effects of flowering time, frequency, successional status, and phylogeny on variation in flowering duration among tree species of seven large families occurring at La Selva, Costa Rica. Because of small sample size, only two-way interaction terms were incorporated. Tests for significance of factors were based on the Type III sums of squares.

Source of variation	df	F	P	R ²
Flowering time (Time)	3	2.74	(*)	
Flowering frequency (Freq)	2	1.00	ns	
Phylogeny	6	0.89	ns	
Successional status (Status)	1	5.65	*	11.3
Time × Freq	3	0.75	ns	
Time × Phylogeny	10	0.62	ns	
Time × Status	1	0.51	ns	
Freq × Phylogeny	9	0.30	ns	
Freq × Status	1	2.08	(**)	
Phylogeny × Status	4	0.22	ns	
Model	43,50	2.27	**	66.2

(*) $P = 0.0529$; (**) $P = 0.1555$; * $P < 0.05$; ** $P < 0.01$; ns = not significant.

revealed new patterns in episodically flowering species. Next, we discuss our results separately in relation to each major parameter of flowering pattern.

Flowering time—We predicted that early successional species should flower any time of the year. This prediction could be realized in two ways. First, the early successional species could flower continually or for a long period. This prediction was realized (described later). Second, early successional species as a group could flower with less seasonality than the late successional species. Indeed early successional species as a group flower across all seasons, but the late successional species do also. Although there are seasonal peaks and troughs, the seasonal patterns are concordant between early and late successional species. This concordance explains continual flowering throughout the year at the community level at La Selva unlike the dry and cloud tropical forests (e.g., Frankie et al., 1974; Opler et al., 1980; Koptur et al., 1988; Wright and Calderon, 1995).

Aseasonal flowering has probably coevolved with the aseasonal availability of pollen vectors. Thus not surprisingly, our prediction that species pollinated by different vectors may flower in different seasons did not hold. This prediction was based on differential abundance of various pollen vectors in the dry and wet seasons in the dry tropical forests (Janzen, 1967; Frankie et al., 1983; Haber and Frankie, 1989). Appar-

ently, seasonality is not as pronounced in the wet tropical forests as we expected.

The prediction that dioecious and hermaphroditic species may differ in their flowering times was also based on the assumption of differential seasonal abundance of generalist pollen vectors that largely pollinate dioecious species (Bawa and Opler, 1975; Bawa, 1980b; Ibarra-Manríquez and Oyama, 1992). Apparently, generalist and specialist vectors are equally abundant across seasons. The long flowering duration of dioecious species discussed later may also constrain seasonal segregation of flowering time in two groups of species. Our results may also have been compromised by two factors. First, we defined flowering time with only two categories, wet or dry season. Second, the small sample sizes for species pollinated by different vectors may have made seasonal patterns difficult to discern, if indeed such patterns exist.

Flowering frequency—We predicted that supra-annual flowering should be less common in early successional as compared to late successional species. In habitats occupied by early successional species, selection of rapid growth, early reproduction, and efficient dispersal (Baker, 1974; Bazzaz, 1979; Bazzaz and Pickett, 1980) is unlikely to favor the evolution of supra-annual flowering, which is unpredictable and occurs once in several years. Early successional habitats are also ephemeral in nature. Because continual flowering accompanies continual fruiting and fruit dispersal, such species can enhance their opportunity to pre-empt transient habitats. Thus, in early successional species, continually flowering species are over-represented in contrast to supra-annually flowering species. Continual flowering, and subsequently continual fruiting, also require a more or less continual supply of photosynthetic resources as well as water. Open sites, such as clearings and treefall gaps, maintain a higher level of soil water and nutrients (Vitousek and Denslow, 1986; Becker et al., 1988).

We predicted that supra-annual flowering should be less common in understory than in canopy species. The massive floral displays over a brief period to recruit pollinators are characteristic of supra-annually flowering species (Ashton et al., 1988; de Jong et al., 1992; Appanah, 1993) that are not likely to be as effective in the canopy, where large masses of flowers act as visual cues over long distances. Momose et al. (1998) also explained the higher frequency of supra-annual flowering species in the canopy of Malaysian forests on the basis of floral displays. Massive display also depends on stored reserves (Bullock and Solís-Magallanes, 1990; Oyama and Mendoza, 1990; Bullock, 1992). Understory species grow in

TABLE 10. Three-way ANOVA of the effects of flowering time, phylogeny, and successional status on variation in flowering duration for species flowering episodically and annually among tree species of seven large families occurring at La Selva, Costa Rica. Tests for significance of factors were based on the Type III sums of squares. Because of small sample size, an interaction effect of time × status was not estimable for annually flowering species.

Source of variation	Episodic				Annual			
	df	F	P	R ²	df	F	P	R ²
Flowering time (Time)	3	1.03	ns		3	6.45	**	
Phylogeny	6	1.63	ns		6	1.29	ns	43.4
Successional status (Status)	1	11.73	**	20.5	1	2.61	ns	
Time × Phylogeny	3	0.61	ns		6	0.61	ns	
Time × Status	1	0.00	ns					
Phylogeny × Status	2	0.18	ns		3	0.89	ns	
Model	17,24	1.96	(*)	58.1	20,21	2.97	**	73.9

(*) $P = 0.0645$; ** $P < 0.01$; ns = not significant.

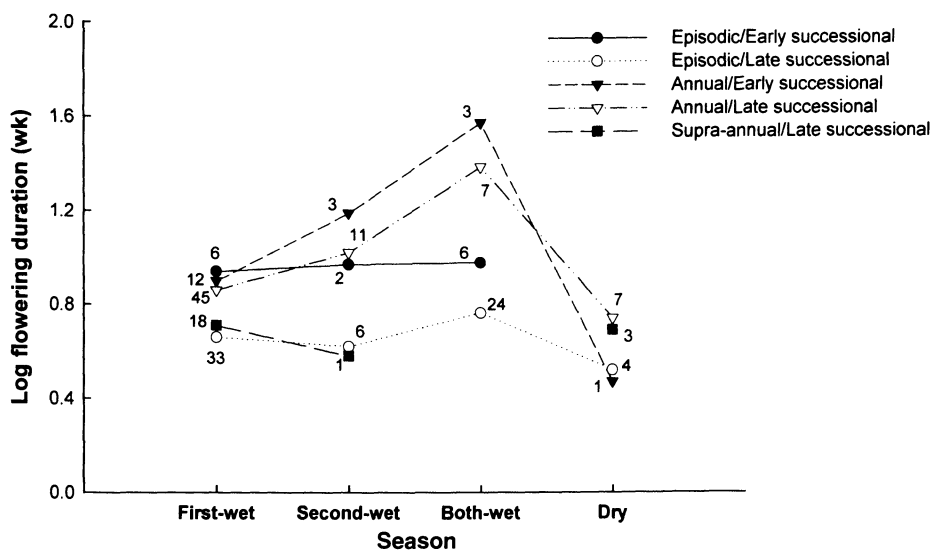


Fig. 3. Mean log flowering duration for each class of flowering time according to flowering frequency and successional status at La Selva, Costa Rica. Numbers near symbols represent the number of species in different classes of flowering frequency and successional status within flowering times.

light-poor environments and are less likely to accumulate reserves than canopy species (see also Momose et al., 1998). Although supra-annual flowering is less common in understory than in canopy species, phylogeny seems to be important in the distribution of supra-annual flowering. More than one-third of canopy species in certain large families such as the Leguminosae and Lauraceae flower supra-annually.

We also predicted that supra-annually flowering species would be rare among dioecious species. The proportion of dioecious species in supra-annually flowering species is low compared to the overall proportion of species with dioecious flowers among La Selva species (9% vs. 23%). This result may reflect disadvantages in association between dioecy and supra-annually flowering. Supra-annual flowering is brief and massive perhaps to attract pollen vectors in species that flower unpredictably at irregular intervals. On the other hand, as argued earlier, sexual selection in dioecious species (Bawa, 1980a, b) may favor extended flowering, facilitated by division of labor (Darwin, 1877). Such disparity in selection pressures for different life history traits is likely to decrease the frequency of dioecy in supra-annually flowering species. Because both sexual system and flowering frequency are constrained by phylogeny, the rarity of supra-annual flowering within con-familial dioecious species or vice versa should further support our argument. In the Moraceae, 88% of species have dioecious flowers, but none of them flower supra-annually. Thus, dioecious flowers may have been selected against in supra-annually flowering species during species divergence, at least in the Moraceae. However, the lack of association between dioecy and supra-annual flowering needs to be further examined because dioecy and flowering frequency may also be correlated with other unexamined ecological characters. Supra-annually flowering species produce seeds occasionally, but when they flower seed crops are huge. Mast fruiting is regarded as a strategy to satiate seed predators and is supposed to have evolved in response to pressure from seed predators (Janzen, 1974; Curran and Webb, 2000). In dioecious species, only female individuals produce seeds, limiting the ability of dioecious populations to satiate seed predators following mast fruiting.

Flowering duration—We predicted that flowering duration should be longer in early successional than in late successional species, in understory species than in canopy species, in dioecious species than in hermaphroditic species, and in species pollinated by specialized pollinators than by generalist pollinators. Our prediction held only for successional status, though we noted expected trends for other groups.

Contrary to our prediction that understory species should flower longer than canopy species, both understory and canopy species at La Selva flower on average for 5.6 wk. Interestingly, previous studies have shown a longer flowering in the understory than in the canopy (Frankie et al., 1974; but see Stiles, 1978) and similarly for shrubs as compared to trees (Opler et al., 1980; Smith-Ramírez and Armesto, 1994). Indirect support for our prediction comes from the relative rarity of supra-annually flowering species that flower briefly in the understory. Our sampling over time may not be adequate to quantify temporal intensity of flowering, thus making it difficult to discriminate massive vs. extended flowering more accurately than the average duration of flowering. On the other hand, at La Selva, photosynthetic responses to light levels, which might be the most important factors limiting growth, differ largely between early and late successional species, but not particularly between understory and canopy species (Fetcher et al., 1994). Thus, understory species may not be particularly constrained by resources as canopy species may be.

Based on energetics and sexual selection, we predicted that species with dioecious flowers should have an extended flowering period. Species with dioecious flowers tended to bloom longer per episode and per year than did those with hermaphroditic flowers. However, longer flowering of dioecious flowers may be confounded or generated spuriously by a suite of ecological correlates of dioecy such as small, inconspicuous flower; small diverse insect vector; fleshy fruit; woody habit; and island habitat (Bawa, 1980b; Renner and Ricklefs, 1995). Sexual system was also constrained by phylogeny, which again was associated with flowering frequency. Thus, identification of the exclusive effect of dioecy on flowering duration should be examined by comparing related species with contrasting sexual systems.

Our prediction that species with generalist vectors would flower longer than those with specialist vectors did not hold, though there was such a trend. The association between flowering duration and pollen vectors is complex because of difficulties in characterizing pollen vectors as generalist and specialist. For example, thrips are small and quite unpredictable in their appearance, but they may be reliable pollinators for *Shorea*, which flower unpredictably at 2–10 yr intervals (Ashton et al., 1988). Despite the wide usage of generalist vs. specialist vectors, distinguishing these two types of vectors is still very difficult without detailed studies (Johnson and Steiner, 2000).

Several aspects of flowering phenology at La Selva also appear to be responsible for lack of a simple, dichotomous pattern of variation in flowering duration in relation to ecological characters. Flowering duration is constrained by flowering frequency and time (Bawa et al., 2003). Selection for male competition in dioecious species or selection by specialized or generalist pollinators may not result in direct, concordant changes in flowering duration, if duration itself is influenced by timing and frequency. For example, Gentry (1974) showed that species with different pollen vectors differed in flowering duration. However, he did not take flowering frequency into account even though species of the Bignoniaceae, the subject of Gentry's studies, vary greatly in flowering frequency.

The pattern of associations between flowering duration and ecological characters changed when flowering frequency was considered. Longer flowering in early successional species than in the late successional applies to only episodically flowering species. In species flowering episodically, early successional species extended flowering twofold longer than the late successional. Episodically flowering species may intrinsically be able to flower over a long period in resource-rich sites because episodic flowering is more or less analogous to continual flowering (Newstrom et al., 1994). *Piper arieianum*, which flowers episodically, has been shown to prolong flowering under higher light levels (Marquis, 1988). Our results suggest that species flowering episodically utilize various resources not only through multiple flowering episodes but also through the extended duration of these episodes. Thus, multiple episodes of flowering may reflect a very specialized feature that is employed by 40–50% of species at La Selva. Information on frequency and ecological diversity of episodically flowering species in other tropical areas is needed to validate the trends observed.

Concluding remarks—In this and the preceding paper, we shift the emphasis in phenology of flowering plants during the last four decades from the timing of flowering to other traits such as the duration and frequency of flowering. We show that the evolution of timing cannot be adequately understood without considering duration and frequency. Unlike previous analyses that demonstrate phylogenetic effects on timing (e.g., Kochmer and Handel, 1986; Smith-Ramírez and Armesto, 1994; Wright and Calderon, 1995), we found timing to be independent of family membership. Furthermore, the duration is not constrained by phylogeny. Both duration and frequency seem to be strongly influenced by energetics (successional status). Sexual selection and pollinators may also influence various flowering parameters, and although we noticed trends in the expected direction, limited sample sizes precluded a thorough analysis. Other factors that we have not fully considered

include seed predation (e.g., Janzen, 1974), seed and fruit maturation time, and seed dispersal agents (e.g., Bawa, 1983; Primack, 1987). Thus, a number of selective forces act on flowering traits, but a preoccupation with timing of flowering has prevented rigorous analysis of the evolution of other variables. Studies of related species with contrasting flowering traits and ecological traits should help reveal the exact forces shaping the evolution and diversity of flowering traits within the context of the hypotheses proposed here.

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