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Phylogenetic patterns among tropical flowering phenologies

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Summary

1 The ability of phylogenetic, water stress and 'shared-pollinator' hypotheses to explain flowering times was tested for the flora of Barro Colorado Island, Panama. Both quantitative (217 species) and qualitative (1173 species) flowering data were used.

2 Descriptive metrics calculated from quantitative flowering data indicated that mean flowering times fell in the final two months of the dry season and the first two months of the wet season for 56% of species and that flowering was concentrated in a short, predictable part of the year for the great majority of species.

3 The 'shared-pollinator' hypothesis predicted that congeners should have temporally segregated flowering times. This hypothesis was rejected for 57 of 59 genera.

4 The water stress hypothesis predicted that species from drier habitats and life forms with limited access to soil water should flower in the wet season. This hypothesis was also rejected.

5 There were, however, strong phylogenetic patterns. Both the mean and the variance of flowering times were similar among congeners. The variance of flowering times was also similar among confamilials, and mean flowering times were concentrated in the wet season for monocotyledons.

Keywords: Barro Colorado Island, comparative method, Panama, tropical forest

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Introduction

Flowering times affect plant success via reproductive processes including pollination and the subsequent timing and success of seed development, dispersal and germination. As a consequence, flowering times have the potential to integrate selection caused by seasonally variable factors that influence reproduction, including moisture, light, temperature, pests, pollinators, seed dispersers, and other plants that share pollinators and seed dispersers (Rathcke & Lacey 1985; Van Schaik *et al.* 1993).

For tropical forest plants, two of these factors, shared pollinators and moisture availability, have received particular attention. When plant species share pollinators, selection may favour temporally segregated flowering to minimize interspecific overlap in flowering times and thus cross pollination and/or competition for limiting pollinators (Stiles 1977; Ashton *et al.* 1988). Alternatively, flowering may be constrained by dry-season water stress with floral anthesis coinciding with the restoration of plant water status following rain, renewed root growth, and/or ongoing dry-season root uptake after leaf abscission (Borchert 1980, 1983; Reich & Borchert 1984).

Recent evidence from other habitats also indicates that flowering times are conservative within evolutionary lineages (Kochmer & Handel 1986; Johnson 1992; Ollerton & Lack 1992). This evidence comes from phylogenetic analyses which determine the proportion of interspecific variation in a trait attributable to phylogeny. Phylogeny has been found to influence a number of plant reproductive traits including seed mass, fruit shape, fruit seediness, flower longevity and fruiting synchrony (Hodgson & Mackey 1986; Mazer 1989, 1990; Stratton 1989; Gorchov 1990; Casper *et al.* 1992; Herrera 1992). Related species are inferred to share traits through common descent (Harvey *et al.* 1995; Westoby *et al.* 1995).

The observation that family membership explains most of the variation in the flowering times of the animal-pollinated angiosperms of Japan and North Carolina is of particular relevance here (Kochmer & Handel 1986). In contrast, several tropical examples suggest that family membership has little impact on flowering phenologies. In south-east Asia, 42 families

include species that flower at irregular, multiyear intervals (Appanah 1985). In Central America, most families include species that flower during the drier season (Janzen 1967; Frankie *et al.* 1974; Croat 1975, 1978; Opler *et al.* 1980). Conversely, a wide array of flowering phenologies may occur within a single tropical family (Gentry 1974).

We use flowering records from Barro Colorado Island (BCI), Panama to evaluate these three hypotheses. The phylogenetic hypothesis predicts that related species will have similar flowering phenologies. This prediction is evaluated for species within genera, families and higher taxa. The water-stress hypothesis predicts that flowering should be limited to the wet season for species with limited access to dry-season soil water reserves. This prediction is evaluated for plant life forms with different access to soil water reserves and for plants from habitats with different dry-season moisture availabilities. The shared-pollinator hypothesis predicts that flowering times should be staggered to minimize flowering overlap and maximize fitness as described above. This prediction is evaluated for congeners because congeners have similar floral morphologies and are most likely to share pollinators. Finally, these hypotheses are largely compatible with one another, and several possible interactions are evaluated.

Materials and methods

BCI (9°9′N, 79°51′W) has a tropical monsoon climate under the Köppen system of climatic classification and supports semideciduous tropical forest with a mature canopy height of 35 m. Mean monthly temperatures are 27 °C in April and 26 °C otherwise. Annual rainfall averages 2600 mm. A 4-month dry season begins in December or rarely November and ends in April or rarely May. Median rainfall between 1 January and 31 March is just 84 mm. Further descriptions of BCI can be found elsewhere (Croat 1978; Leigh *et al.* 1982; Windsor 1990).

Two data sets were used. Quantitative data from passive litter traps permitted detailed analyses of monthly distributions of flower records, but were largely limited to trees and lianas from closed canopy forest. In contrast, qualitative descriptions of flowering times taken from Croat (1978) only permitted analyses of summary statistics, but included additional species, life forms and habitats.

QUALITATIVE FLOWER RECORDS

Croat (1978) lists the months in which flowering occurs for 1173 of the 1265 angiosperms then recorded for BCI. His descriptions summarize '... observations made during more than three years in Panama and a survey of 50 000 herbarium specimens from BCI and adjacent areas.' Croat (1978; p. 30) further states that '... the data represent what is thought to be the normal phenological variation for each species...In the better-known species, 95% or more of the flowering or fruiting probably falls within the timespan indicated.'

These qualitative data were used to estimate flowering season length and mean flowering times following procedures developed by Kochmer & Handel (1986). Flowering season length was simply the number of months in which flowering was recorded. Central tendency, or in the words of Kochmer & Handel (1986) mean timing, was the 'midpoint of extreme recorded dates of flowering.' Midpoints are arbitrary for species that flower year-round. The treatment of the 279 such species is described for each analysis of flowering midpoints. Midpoints are problematical when flowering occurs discontinuously in two or more periods separated by one or more months without flowering. The 38 species that flowered discontinuously were therefore excluded from all analyses of qualitative flowering phenologies. Introduced species were also excluded throughout.

QUANTITATIVE FLOWER RECORDS

All flowers captured in 230 litter traps were identified to species each week from 1 January 1987 through 31 December 1991. Traps were located in the BCI forest dynamics plot (200 traps) and as part of a long-term forest irrigation experiment (only the 30 traps in control plots were used here). Both sites have escaped human disturbance for > 500 years (Piperno 1990) and support mature forest. Further site descriptions can be found elsewhere (Hubbell & Foster 1990; Wright & Cornejo 1990a,b). Traps were located in a stratified random manner at both sites with minimum distances between traps of 15.7 m on the forest dynamics plot and 10 m on control plots. Traps were constructed from 1 mm mesh screen suspended from a PVC frame. Trap surface area was 0.5 m^2 in the forest dynamics plot and 0.25 m^2 in the control plots.

We defined flower records to be one or zero if flowers were present or absent, respectively, for each species, week and trap. Most lowland tropical flowers live a single day (Primack 1985), and flower records reflect the timing of anthesis. We analysed flower records summed over months and years. Species with < 10 flower records were excluded.

The quantitative flower records were used to obtain a second independent estimate of flowering season length and mean flowering times. Flowering season length was defined as the number of months in which the number of flower records was > 2% of the total. The 2% cut-off was arbitrarily chosen to eliminate flowers temporarily trapped in aerial litter that may have fallen to the ground long after anthesis.

Vector algebra was required to calculate mean flowering times because flowering occurred year-round. Under these circumstances, a linear or Julian time scale is unworkable because an origin must be

identified and all subsequent calculations depend on the choice of origin. Vector algebra avoids this problem because the year is represented by a rotation of 360° with arbitrary origin (by convention 1 January equalled 0° or 360°). Mean flowering times were calculated as the angle of the mean vector, ϕ, where

$$\phi = \arctan(y/x) \quad \text{if } x > 0 \tag{1a}$$

$$\text{or} \quad \phi = 180° + \arctan(y/x) \quad \text{if } x < 0; \tag{1b}$$

$x = \Sigma n_i \cos \phi_i$, $y = \Sigma n_i \sin \phi_i$, where n_i is the number of flower records in month i and ϕ_i is the midpoint of month i expressed as an angle. The length of the mean vector, r, provides an additional measure of the concentration of flowering times where

$$r = (x^2 + y^2)/\Sigma n_i. \tag{2}$$

The length of the mean vector ranges between zero (when equal numbers of flower records occur in each month) and one (when all flower records occur in a single month).

Two examples illustrate these calculations. Flower records for *Triplaris cumingiana* (Polygonaceae) occurred between February and April with a sharp symmetrical peak in early March (Table 1). The angle of the mean vector, 66°, corresponds closely to early March, and the length of the mean vector, 0.95, is close to one. In contrast, flower records for *Guatteria dumetorum* (Annonaceae) occurred in all months with large numbers of records in at least 9 months (Table 1). The angle of the mean vector, 358°, falls in December which is close to the middle of the nine-month period of high flower production, and the length of the mean vector is just 0.19. Equations 1 and 2 are explained in greater detail in another context by Batschelet (1981; pp. 7–18).

QUANTITATIVE AND QUALITATIVE PHENOLOGIES COMPARED

The two estimates of flowering season length and central tendency provide an opportunity to compare and evaluate the two independent methods used to assess flowering phenologies. Flowering season length is a linear variable, and a paired t-test was used to compare flowering season lengths. A circular correlation analysis (Batschelet 1981) was used to compare flowering midpoints derived from Croat (1978) with mean flowering times calculated from eqn 1. Species that Croat (1978) recorded flowering year-round were omitted from the correlation analysis.

THE SHARED-POLLINATOR HYPOTHESIS

Null model analyses were used to determine whether the level of flowering overlap observed among congeners differed significantly from chance expectation. Null models used to evaluate flowering overlap for both qualitative and quantitative flowering data have been reviewed elsewhere (Ashton *et al.* 1988; Pleasants 1990), and the appropriate null models recommended by these investigators are used here.

For qualitative flowering data, Model three of Ashton (1988) was used. The observed number of months of flowering overlap summed over all congeneric species pairs was compared with 99 simulated values. Simulations randomized the timing of flowering midpoints while preserving the length of the flowering season observed for each species s (L_s) and the overall length of the flowering season observed for all congeners (L_g). In practice, this null model has two limitations. First, if $L_s = L_g$ for two or more species, then the scaling factor used to preserve L_g in simulations equals zero and all simulations have a single outcome (see eqns 1 and 2 in Ashton *et al.* 1988). This difficulty could be avoided by eliminating all but one species with $L_s = L_g$ because such species make a constant contribution to flowering overlap. The second limitation affects two-species genera. Simulated and observed overlap are equal for two-species genera because the simulations preserve L_g and each L_s. Null model analyses of qualitative flowering times were therefore limited to genera with at least two species with $L_s < L_g$ and at least three species overall.

For quantitative flowering data, the mean pairwise overlap model of Pleasants (1980, 1990) was used. An overlap index (Pianka 1974) was calculated for each pairwise combination of species, and the mean observed value was compared with 99 simulated values. Simulations randomized mean flowering times (eqn 1) while preserving the observed distribution of flower records around the mean for each species and the overall length of the flowering season observed

Table 1 Flowering of selected species from Barro Colorado Island, Panama. Entries are numbers of trap records compiled by month from 260 weekly censuses of 230 traps (see text). The complete data set for 217 species is available from the authors

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Annonaceae												
Guatteria dumetorum	160	167	175	183	89	42	69	123	155	170	174	179
Polygonaceae												
Coccoloba coronata	0	0	0	0	1	0	3	6	0	0	0	0
Coccoloba manzanillensis	1	0	0	0	0	0	4	13	9	0	0	0
Coccoloba parimensis	1	1	1	10	24	26	0	0	1	0	0	0
Triplaris cumingiana	0	120	208	22	1	0	0	0	0	0	0	0

for all congeners. Preservation of the overall length of the flowering season for each genus also invalidates this null model for two-species genera. Analyses were therefore limited to genera with three or more species for which each forest species recorded as an adult on BCI was represented by $\geqslant 10$ trap records.

For both types of null model analyses, evidence consistent with staggered (aggregated) flowering times occurred when the observed flowering overlap metric was smaller (greater) than 95 simulated values.

THE WATER-STRESS HYPOTHESIS

Contingency analyses were used to determine whether groups of species with differential access to dry-season water supplies had different flowering midpoints. Habitat and life form were used as proxies for dry-season water supplies. Species with flowering midpoints in the dry season (mid-December through April) were contrasted with species with flowering midpoints in the wet season (the remainder of the year). With respect to habitat, we predicted that the proportion of species with flowering midpoints in the dry season would be greatest in marshes and swamps which provide water year-round, intermediate in clearings and large tree-fall gaps which have intermediate dry-season soil water content, and least in closed-canopy forest which is driest. Greater soil water availability in tree-fall gaps than in closed canopy forest has been noted on BCI and also at La Selva, Costa Rica (Robichaux *et al.* 1984; Vitousek & Denslow 1986; Becker *et al.* 1988). With respect to life form, we predicted that the proportion of species with flowering midpoints in the dry season would be greatest for trees and lianas which have relatively deep root systems, intermediate for terrestrial herbs and shrubs which have relatively shallow root systems, and least for epiphytes which lack access to soil water reserves. Root excavations and studies of plant water relations confirm that terrestrial herbs and shrubs tend to have shallow root systems and high levels of dry-season water stress relative to trees and lianas on BCI (Rundel & Becker 1987; Becker & Castillo 1990; Mulkey, Smith & Wright 1991; Wright 1991, 1992, in press; Wright *et al.* 1992). Species descriptions from Croat (1978) were used to assign each species to a habitat and life form. Species that flowered year-round were excluded from both analyses. Hemi-epiphytes and strangler figs that germinate as epiphytes but later root in the soil were excluded from the life form analysis, as were four saprophytic species.

The water-stress hypothesis was not evaluated for the quantitative flower records from traps because the data were largely limited to two deeply rooting life forms (trees and lianas) from a single habitat (closed-canopy forest).

THE PHYLOGENETIC HYPOTHESIS

Contingency analyses were performed to determine whether phylogeny influenced qualitative flowering midpoints. The analysis was based on a partition of the heterogeneity log-likelihood ratio observed for the seasonal distribution of flowering midpoints among families (G_{Hf}) into components contributed by higher taxonomic levels. This partition is made possible by the additive properties of log likelihood ratios. It is easily demonstrated that

$$G_{\mathrm{Hf}} = \Sigma_{\mathrm{o}} G_{\mathrm{Hf(o)}} + \Sigma_{\mathrm{sc}} G_{\mathrm{Ho(sc)}} + \Sigma_{\mathrm{c}} G_{\mathrm{Hsc(c)}} + G_{\mathrm{Hc}}, \qquad (3)$$

where the subscripts Hf(o), Ho(sc), Hsc(c) and Hc specify heterogeneity log-likelihood ratios calculated for families within orders, orders within subclasses, subclasses within classes, and classes, respectively. Generally, this partition could be used to identify taxonomic patterns for any discrete data. The partition generates multiple tests, and the Bonferonni procedure was used to protect against Type I statistical error. Families with fewer than nine native species with known flowering phenologies were excluded to maintain minimum expected frequencies of about five. The analyses were repeated without species that flowered year-round and then again after assigning a midpoint at random for such species.

A taxonomy that did not accurately reflect phylogeny would clearly compromise this analysis. There is wide agreement that the monocotyledons are monophyletic; however, polyphyly and paraphyly have been identified in many other angiosperm taxa (reviewed by Chase *et al.* 1993). We therefore restricted our analysis to a partition of G_{Hf} into components contributed by class (G_{Hc}) and by families within classes ($\Sigma_{\mathrm{c}} G_{\mathrm{Hf(c)}}$), where the classes were monocotyledons and dicotyledons as defined by Cronquist (1981).

An alternative phylogeny is suggested by a recent exploratory analysis of DNA sequences from 499 species representing all major taxa of seed plants (Chase *et al.* 1993). This analysis confirmed that the monocots are monophyletic. The dicots, however, were divided into eudicots and 'primitive' dicots. The 'primitive' dicots and monocots shared uniaperturate pollen and were more closely related to one another than to the eudicots which had triaperturate pollen. The eudicots were further divided into Asteridae, Rosidae and several smaller clades. The phylogenetic positions of the monocots, 'primitive' dicots, eudicots, Asterids and Rosids have been confirmed by other recent morphological and molecular analyses (reviewed by Chase *et al.* 1993). We therefore repeated the analysis using this tentative phylogeny.

A hierarchical log-linear analysis (Sokal & Rohlf 1981) was used to evaluate the interaction between life form, taxa and the seasonal distribution of flowering midpoints. The analysis was restricted to a comparison of monocots and dicots to maintain expected

frequencies of five. The analysis was also restricted to a comparison of epiphytes and terrestrial herbs because trees, shrubs and lianas are poorly represented within the monocots (just 32 species).

A repeated measures analysis of variance was performed for the quantitative flower records. Repeated measures occurred on months, taxonomic units were grouping variables, and species were subjects. The interaction between taxa and month is of greatest interest here, with a significant interaction indicating that the timing of flowering differed among taxa. Significant main effects of month and taxa would indicate that numbers of flower records varied among months and taxa, respectively. The large numbers of families and genera precluded a nested analysis, and separate analyses were performed for families and genera with $\geqslant 3$ and $\geqslant 2$ species, respectively. The Greenhouse–Geisser correction was used to adjust degrees of freedom downward to protect against violations of the compound symmetry assumption of repeated measures ANOVA.

The index of flowering concentration (eqn 2) is a linear variable, and a nonparametric Kruskal–Wallis analysis was used to test the null hypothesis that family membership influenced flowering concentration.

Results

QUANTITATIVE FLOWER RECORDS

Flowers of 217 species were encountered 10 or more times in litter traps. At least eight species had mean flowering dates in any given calendar month (Fig. 1). Nonetheless, mean flowering dates were concentrated in February and March which are the driest months of the year and in April and May when the wet season begins. Flowering was highly concentrated in time for most species although a few species flowered year-round (Fig. 1).

QUALITATIVE AND QUANTITATIVE PHENOLOGIES COMPARED

There was close agreement between flowering midpoints derived from Croat (1978) and mean flowering times calculated from trap records ($R_+ = 0.60$, $P < 10^{-9}$, $n = 182$ species). Note that the circular correlation coefficient, R_+, differs from a linear regression coefficient and is unrelated to the proportion of variation explained (Batschelet 1981). The close agreement between the two independent estimates of central tendency validates many of the following analyses.

In contrast, the two independent estimates of the length of the flowering season differed substantially (paired $t = 8.365$, $P < 0.001$). Flowering season length averaged 7.0 and 5.0 months for trap records and Croat's qualitative records, respectively. This

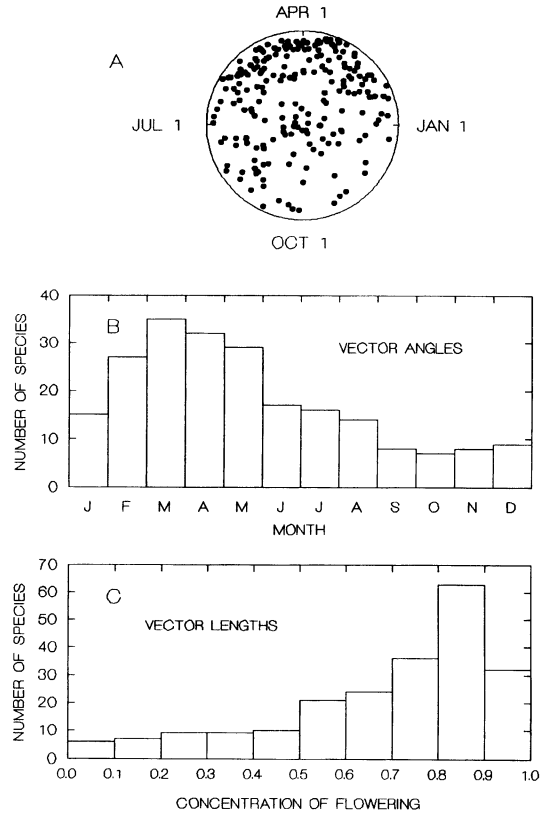

Fig. 1 Flowering phenologies for the 217 angiosperm species recorded $\geqslant 10$ times in litter traps. (a) Phenologies as unit vectors whose angles and lengths correspond to mean flowering dates and the concentration of flowering times, respectively. (b) The distribution of mean flowering dates among months for the 217 species. (c) The distribution of the concentration of flowering times. Mean flowering dates and the concentration of flowering times were calculated from flower trap records using eqns 1 and 2, respectively.

difference would be even larger if months with $< 2\%$ of total flower records had been included in the estimate of flowering season length based on trap records. Croat (1978) clearly underestimated flowering season length for many species. Analyses of flowering season length and the concentration of flowering times were therefore restricted to trap records.

THE SHARED-POLLINATOR HYPOTHESIS

The null model analysis of overlap for qualitative flowering data was performed for 59 genera. The observed flowering overlap was greater than 95% of the simulated values for the following genera: *Calathea*, *Cassia*, *Cissus*, *Cordia*, *Cyperus*, *Heliconia*, *Paspalum*, *Passiflora*, *Philodendron*, *Piper and Psychotria*. For these 11 genera, flowering times were temporally aggregated within the flowering season observed for the genus on BCI. Interestingly, *Heliconia* species have temporally aggregated flowering times on BCI and temporally segregated flowering at La Selva, Costa Rica (Stiles 1977). Evidence consistent with temporally segregated flowering was obtained for the following genera on BCI: *Casearia*, *Epidendrum*, *Inga*,

Table 2 Qualitative flowering phenologies for selected genera for which observed flowering overlap was less than 95 simulated values. Entries of one represent months in which the species flowers. Visual inspection suggests staggered flowering consistent with the 'shared-pollinator' hypothesis for *Casearia and* possibly *Paullinia*, but not *Maxillaria*. Data from Croat (1978)

	J	F	M	A	M	J	J	A	S	O	N	D
Casearia aculeata	0	0	1	1	0	0	0	0	0	0	0	0
C. guianensis	0	0	1	1	1	0	0	0	0	0	0	0
C. corymbosa	0	0	0	1	1	0	0	0	0	0	0	0
C. arborea	0	0	0	0	0	1	1	0	0	0	0	0
C. commersoniana	0	0	0	0	0	1	1	1	1	0	0	0
C. sylvestris	0	0	0	0	0	0	0	1	1	1	1	1
C. arguta	1	0	0	0	0	0	0	0	0	1	1	1
Maxillaria crassifolia	0	0	0	1	1	1	1	1	1	1	1	0
M. alba	0	0	0	0	1	1	1	1	1	1	1	0
M. neglecta	0	0	0	0	1	1	1	1	1	1	1	0
M. uncata	1	0	0	0	1	1	1	1	1	1	1	1
M. powellii	1	0	0	0	0	0	0	0	0	1	1	1
M. friedrichsthalii	1	0	0	0	0	0	0	0	0	0	0	1
M. camaridii	1	1	1	1	0	0	0	0	0	0	0	1
M. variabilis	1	1	1	1	0	0	0	0	0	0	0	1
Paullinia pinnata	0	0	0	0	0	1	1	1	0	0	0	0
P. glomerulosa	0	0	0	0	0	1	1	1	1	1	0	0
*P. baileyi**	0	0	0	0	0	0	0	1	1	0	0	0
P. rugosa	0	0	0	0	0	0	0	1	1	1	1	0
P. fibrigera	1	1	0	0	0	0	0	0	0	1	1	1
P. turbacensis	1	1	0	0	0	0	0	0	0	0	1	1
P. fuscescens	1	1	1	1	0	0	0	0	0	0	0	1
P. bracteosa	1	1	1	1	1	1	1	1	0	0	0	1

The flowering phenology of *P. pterocarpa* is unknown.

*Incorrectly recorded as flowering in March and April by Croat (1978). August and September flowering agrees with trap records and personal observation.

Maxillaria, *Paullinia* and *Rhynchospora*. Observed flowering overlap was less than 97 simulated values for *Paullinia* and less than all 99 simulated values for the five remaining genera.

This last result must be interpreted cautiously. Observed flowering overlap will be minimal whenever the variance in the number of species flowering in each month i (S_i) is minimal [to prove this, evaluate flowering overlap for constant S_i and for S_i with an arbitrarily small variance, where flowering overlap $= \Sigma S_i(S_i - 1)/2$]. Several flowering patterns will minimize the variance in S_i. One possibility is the temporally segregated or staggered flowering pattern predicted by the shared-pollinator hypothesis. Another possibility is that groups of equal numbers of species flower in different seasons. Because more than one flowering pattern is consistent with significantly small values of flowering overlap, interpretation of this result must include visual inspection of the observed flowering patterns.

This inspection suggests that three of the genera with significantly small values of flowering overlap (*Epidendrum*, *Inga* and *Maxillaria*) have groups of roughly equal numbers of species with similar flowering phenologies. This pattern is clearest for *Maxillaria* with four species flowering in the wet season, two in the dry season, and two in the wet-to-dry season transition (Table 2). A fourth genus, *Rhynchospora*, had too few species (4) to evaluate. Only two genera, *Casearia and* possibly *Paullinia*, have the staggered flowering patterns predicted by the shared-pollinator hypothesis.

The null model analysis of overlap for quantitative flowering data was performed for the three genera for which each of the three or more species recorded from BCI was represented by $\geqslant 10$ flower records. Observed flowering overlap was smaller than 94, 91 and 66 of the 99 values simulated for *Hiraea*, *Virola and Cordia*, respectively. Again, there is little evidence for the staggered flowering patterns predicted by the shared-pollinator hypothesis.

THE WATER-STRESS HYPOTHESIS

Overall 45% of species had flowering midpoints in the dry season. The seasonal distribution of flowering midpoints was unaffected by habitat (Table 3,

Table 3 Number of species inhabiting forest, artificial clearings, and marshes and swamps with flowering midpoints in the dry and wet seasons. The dry season extends from mid December through April. The wet season includes the remainder of the year

Habitat	Dry season	Wet season
Forest	264	325
Artificial clearings*	64	84
Ever-wet habitats	37	39

*Artificial clearings are maintained by man.

Table 4 Numbers of species from different life forms with flowering midpoints in the dry and wet seasons. The dry season extends from mid December through April. The wet season includes the remainder of the year

Life Form	Dry season	Wet season
Epiphyte	51	53
Terrestrial Herb	59	118
Liana/Vine	95	79
Shrub	52	65
Tree	106	127

$G_H = 0.60$, d.f. $= 2$, $P = 0.74$), but differed among life forms (Table 4, $G_H = 17.1$, d.f. $= 4$, $P = 0.002$). The life form differences were, however, poorly associated with dry-season moisture availability. In particular, flowering season midpoints fell in the dry season for 49% of epiphyte species even though epiphytes lack access to soil water. Numbers of species differ between Tables 3 and 4 because hemiepiphytes and saprophytes were excluded from the life form analysis and the habitat affinities of a handful of species are poorly known.

THE PHYLOGENETIC HYPOTHESIS

The 32 families with nine or more native species with known qualitative flowering phenologies included a total of 797 species (Table 5). The qualitative results of the following analyses were robust with respect to the treatment of the 189 species that flowered year-round (either excluded or assigned a flowering midpoint at random), and the results presented include these species (Tables 5–7). Many families had similar numbers of species with flowering midpoints in each season, and no family was restricted to a single season (Table 5). Nonetheless, the seasonal distribution of flowering midpoints varied significantly among families ($G_{Hf} = 85.60$, d.f. $= 31$, $P < 0.001$).

The partition of G_{Hf} into components contributed by higher taxa is presented in Table 6. Part A of Table 6 contrasts monocots and dicots as defined by

Table 5 Numbers of species with flowering midpoints in the dry and wet seasons for Barro Colorado Island, Panama. The dry season extends from mid-December through April. The wet season includes the rest of the year. Families are organized into higher clades defined by the strict consensus tree obtained from an exploratory phylogenetic analysis of DNA from 499 species of seed plants (Chase *et al.* 1993). Only families with at least nine native species with known phenologies are included. Species that flowered discontinuously were excluded, those that flowered year-round were assigned to a season at random

			Number of species	
Pollen type	Clade	Family	dry	wet
Uniaperturate	Magnoliales	Annonaceae	3	6
Uniaperturate	Palaeoherb	Piperaceae	20	8
Uniaperturate	Monocots	Araceae	10	31
Uniaperturate	Monocots	Arecaceae	5	10
Uniaperturate	Monocots	Cyperaceae	7	19
Uniaperturate	Monocots	Poaceae	20	44
Uniaperturate	Monocots	Orchidaceae	38	41
Uniaperturate	Monocots	Bromeliaceae	5	12
Uniaperturate	Monocots	Marantaceae	2	10
Uniaperturate	Monocots	Zingiberaceae	1	8
Triaperturate	Asteridae	Asteraceae	20	18
Triaperturate	Asteridae	Apocynaceae	7	11
Triaperturate	Asteridae	Asclepiadaceae	3	6
Triaperturate	Asteridae	Boraginaceae	6	5
Triaperturate	Asteridae	Rubiaceae	17	48
Triaperturate	Asteridae	Acanthaceae	12	1
Triaperturate	Asteridae	Bignoniaceae	11	17
Triaperturate	Asteridae	Solanaceae	9	11
Triaperturate	Caryophyllidae	Polygonaceae	4	5
Triaperturate	Rosidae	Bombacaceae	7	2
Triaperturate	Rosidae	Passifloraceae	7	2
Triaperturate	Rosidae	Moraceae	9	16
Triaperturate	Rosidae	Euphorbiaceae	11	14
Triaperturate	Rosidae	Caesalpiniaceae	6	8
Triaperturate	Rosidae	Mimosaceae	21	14
Triaperturate	Rosidae	Fabaceae	31	25
Triaperturate	Rosidae	Melastomataceae	12	21
Triaperturate	Rosidae	Myrtaceae	3	7
Triaperturate	Rosidae	Malpighiaceae	8	11
Triaperturate	Rosidae	Sapindaceae	18	7
Triaperturate	Not treated	Clusiaceae	4	7
Triaperturate	Not treated	Flacourtiaceae	6	9

Table 6 The contribution of higher taxa to heterogeneity in the seasonal distribution of flowering midpoints. Part A partitions heterogeneity among families and classes defined by Cronquist (1981). Part B partitions heterogeneity among families and higher clades defined by the strict consensus tree obtained from an exploratory phylogenetic analysis of DNA from 499 species of seed plants (Chase *et al.* 1993)

Source	G	d.f.	P
Part A			
Classes	14.90	1	<0.001
Families (Dicots)	56.97	23	<0.001
Families (Monocots)	13.74	7	0.056
Part B			
Monocots vs. Eudicots	13.11	1	<0.001
Asterids vs. Rosids (Eudicots)	3.77	1	0.052
Families (Asterids)	24.89	7	0.001
Families (Rosids)	20.05	10	0.029
Families (Monocots)	13.74	7	0.056

Bonferonni adjusted significance levels are 0.017 and 0.01 for parts A and B, respectively.

Cronquist (1981). The seasonal distribution of flowering midpoints was homogeneous among families within the monocots, with flowering midpoints occurring in the wet season for a majority of species in each family (Table 5). In contrast, there was significant heterogeneity among families within the dicots. Dicot families for which more than 70% of species have flowering midpoints in a single season included the Rubiaceae (wet season) and the Acanthaceae, Piperaceae and Sapindaceae (dry season). The seasonal distributions of flowering midpoints also differed between classes with flowering midpoints in the dry season for 33% and 48% of monocots and dicots, respectively.

Part B of Table 6 partitions G_{Hf} into components contributed by higher taxa for the phylogeny tentatively proposed by Chase *et al.* (1993). Five families from the previous analysis were excluded. There were two reasons for exclusion. First, the Clusiaceae and Flacourtiaceae were not considered by Chase *et al.* (1993). Secondly, three higher clades were represented by a single family. When this occurs, it is impossible to determine whether heterogeneity occurs among families within the higher clade or among higher clades. To avoid this difficulty, the three isolated families were excluded (Piperaceae, Annonaceae and Polygonaceae). There was significant heterogeneity among the seasonal distributions of flowering midpoints for the remaining 27 families ($G_{Hf} = 75.55$, d.f. = 26, $P < 0.001$). Significant heterogeneity also occurred among families within the Asteridae and between the monocots and eudicots; however, the null hypothesis of homogeneity could not be rejected for families within the monocots, families within the Rosidae, nor the contrast of Asterids and Rosids within the eudicots (Table 6, Part B).

The difference in flowering phenologies noted between dicots and monocots held across life forms. The three–way interaction between taxa, life form and flowering season was not significant ($G_H = 2.40$, d.f. = 1, $P = 0.12$). The two–way interactions were each significant ($P < 0.001$), and, relative to the dicots, disproportionate numbers of monocots had flowering midpoints in the wet season regardless of life form (Table 7).

The two repeated measures ANOVAs identified significant differences in numbers of flower records among months and among families and genera (Tables 8 and 9). Peak numbers of flower records occurred between February and May (the month effect in Tables 8 and 9). Croat (1975, 1978) also noted a broad peak in flower production during these months on BCI. Differences in numbers of flower records among taxa (the between-species effect in Tables 8 and 9) may be related to differences in the population densities of reproductives, flowering frequency and/or numbers of flowers produced per flowering event. The interaction between taxa (family or genus) and month is of greater interest here because this interaction addresses the hypothesis that flowering phenologies are independent of family and genus membership.

The statistical significance of these interactions must be interpreted cautiously because the degrees of freedom and therefore the power of the tests were exceptionally large (Tables 8 and 9). In particular, the

Table 7 Numbers of species of epiphytes and terrestrial herbs with flowering midpoints in the dry and wet seasons for Monocotyledons and Dicotyledons. The dry season extends from mid-December through April. The wet season includes the rest of the year

Life form	Dry season	Wet season
Monocotyledons		
Epiphytes	50	64
Herbs	43	120
Dicotyledons		
Epiphytes	14	15
Herbs	66	73

Table 8 Repeated measures analysis of variance of flower records for genera. Analyses are for logarithms of monthly flower records plus one. Within-subjects significance levels were determined after making the Greenhouse–Geisser adjustment to degrees of freedom

Source	Sum-of-squares	d.f.	Mean square	F
Between species				
Genus	364.1	31	11.7	1.27*
Error	469.8	51	9.2	
Within species				
Month	117.0	11	10.6	12.74***
Month × Genus	729.2	341	2.2	2.56***
Error	468.2	561	0.83	

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

Table 9 Repeated measures analysis of variance of flower records for families. Analyses are for logarithms of monthly flower records plus one. Within-subjects significance levels were determined after making the Greenhouse–Geisser adjustment to degrees of freedom

Source	Sum-of-squares	d.f.	Mean square	F
Between species				
Family	598.5	30	19.9	1.69*
Error	1740.9	148	11.8	
Within species				
Month	264.8	11	24.1	18.64***
Month × Family	647.4	330	2.0	1.52**
Error	2101.9	1628	1.29	

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

statistically significant F-value associated with family membership was very small (Table 9). This suggests doubtful biological significance. Variance components confirm this suspicion. The proportion of total within-species variance associated with the interaction between family and month was just 0.069. In contrast, the within-species variance component associated with the interaction between genus and month was 0.272, nearly four times greater. Genus membership had a much stronger effect on flowering phenologies than did family membership. Inspection confirms that flowering phenologies tend to be similar among congeners but vary widely among confamilials.

Nevertheless, the concentration of flowering times (eqn 2) differed among families (Kruskal–Wallis test statistic $= 51.8$, d.f. $= 30$, $P = 0.008$). The least synchronous families included the Hippocrataceae, Moraceae and Myristicaceae in which all species produced substantial numbers of flowers in $\geqslant 8$ months. The most synchronous families included the Boraginaceae, Lauraceae and Polygonaceae in which all species produced substantial numbers of flowers in $\leqslant 5$ months.

Discussion

The phylogenetic and shared-pollinator hypotheses generate conflicting predictions about the evolutionary persistence of phylogenetic patterns. If shared pollinators selected for temporally segregated flowering among closely related species, then phylogenetic patterns would diminish rapidly over evolutionary time. The two examples of temporally segregated flowering from tropical forests involve congeneric plants, specifically hummingbird-pollinated *Heliconia* from Costa Rica and thrip-pollinated dipterocarps from a subsection of the genus *Shorea* from Malaysia (Stiles 1977; Ashton *et al.* 1988). In contrast, temporally segregated flowering was not characteristic of BCI congeners; in fact, observed flowering was consistent with nonrandom temporal segregation for just two of the 59 genera evaluated. This result should not be taken as evidence against the shared-pollinator hypothesis because the pollinators of the great majority of BCI species are unknown (D. W. Roubik, personal communication) and the possibility that BCI congeners share pollinators remains an inference based on similarities in floral morphology. Rather, the rarity of temporally segregated flowering among BCI congeners indicates that shared-pollinator selection is not a general phenomenon obscuring phylogenetic patterns in flowering times.

Dry-season water stress constrains the flowering phenologies of many plants in seasonal tropical forests (Borchert 1980; Reich & Borchert 1984). This raises the possibility that nonrandom distributions

of higher taxa with respect to dry-season moisture availability might explain apparent phylogenetic patterns in flowering phenologies. This possibility was evaluated for differences in dry-season moisture availability observed among habitats and also among plant life forms. Flowering seasonality was independent of habitat within BCI (Table 3). In contrast, flowering seasonality varied among life forms (Table 4), however, the observed variation was inconsistent with differences in dry-season moisture availability among life forms. Even though moisture availability is not the mechanism, phylogenetic patterns in life form might still explain phylogenetic patterns in flowering phenologies. This possibility was discounted for classes (Table 7), and we conclude that habitat and life form are unlikely to confound phylogenetic analyses of BCI flowering phenologies.

In contrast to the generally negative results of our analyses for the shared-pollinator and water-stress hypotheses, significant phylogenetic effects emerged from most but not all of our analyses of BCI flowering phenologies. We have still to reconcile discrepancies among the various phylogenetic analyses.

An overview of the phylogenetic analyses is required to reconcile their results. Phylogenetic analyses were performed at several taxonomic levels and with two types of data. Here, data types refer to summary statistics vs. distributions of quantitative flower records among months. The discrepant results emerged between data types within a single taxonomic level. Specifically, family membership had biologically significant effects for analyses involving summary statistics (flowering concentrations and midpoints, Table 6) but not for analyses involving monthly distributions of flower records (Table 9). Differences in the identities of the species analysed cannot explain this discrepancy because the same 179 species were used for the Kruskal–Wallis analysis of the concentration of flowering times and the repeated measures analysis of monthly distributions of flower records among families. Rather, the analyses have different sensitivities as illustrated in Fig. 2. Analyses of a summary statistic are obviously only sensitive to variation in that statistic. In contrast, analyses of the monthly distributions of flower records are sensitive to all sources of variation that might obviate phylogenetic effects (Fig. 2).

The four species of Polygonaceae encountered in traps illustrate this difference (Table 1). Each species produced significant numbers of flowers in $\leqslant 3$ months; however, mean flowering dates varied widely falling in March, May, July and August. Thus, the Polygonaceae provide strong evidence that family membership affects the temporal concentration of flowering, but little evidence that family membership affects mean flowering times. For the quantitative flower records, the summary statistics used here are the first (eqn 1) and second (eqn 2) moments of the monthly distributions of flower records. For the qualitative flower records, the summary statistics are the best approximations of the first (flowering midpoint) and second (flowering season length) moments available. The discrepant results obtained for the various analyses of family membership (as illustrated by the Polygonaceae) suggest that phylogenetic effects can affect just one moment of a flowering distribution (Fig. 2).

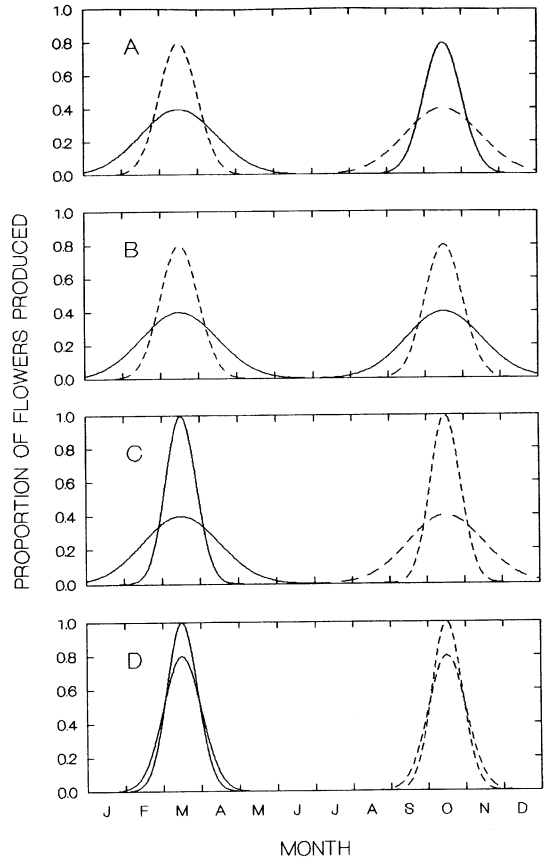

Fig. 2 Hypothetical distributions of flowers among months for four species from two higher taxa. Solid and dashed lines represent species from different higher taxa. Examples have been chosen to illustrate the sensitivities of different phylogenetic analyses. (a) Mean flowering dates and flowering synchrony both differ widely between species within taxa. There is no taxonomic effect. (b) Species within taxa have similar concentrations of flowering times, but dissimilar mean flowering dates. An analysis of the second moment of flowering times would detect this taxonomic effect. (c) Species within taxa have similar mean flowering dates, but dissimilar concentrations of flowering times. An analysis of the first moment of flowering times would detect this taxonomic effect. (d) Mean flowering dates and concentrations of flowering times are both similar for species within taxa. The repeated measures analysis of flower records will detect this taxonomic effect (as will an analysis of the first moments of flowering times). Note that analyses of one moment of a distribution may identify significant taxonomic effects when large within-taxa variation remains (b,c).

Previous phylogenetic treatments of plant reproductive phenologies have been limited to analyses of summary statistics. These include analyses of mean flowering times (Kochmer & Handel 1986), mean flower longevity (Stratton 1989) and standard deviations of fruiting times (Gorchov 1990). These analyses leave open the possibility that temporal distributions of repro-

ductive activity vary widely within taxa as in Fig. 2(B) and (C). Additional analyses of full temporal distributions of reproductive activity will be required to evaluate phylogenetic effects on reproductive phenologies more completely.

We can now evaluate phylogenetic effects at several taxonomic levels for BCI flowering phenologies. Phylogenetic effects were strongest among congeners. A repeated measures analysis that included 83 species from 32 genera demonstrated that congeners share similar monthly distributions of flower records on BCI (Table 8). Limited phylogenetic effects were present among confamilials as discussed above. Finally, class membership had significant effects on the seasonal distribution of flowering midpoints (Table 6), however, a more complete evaluation must await monthly distributions of flower records for additional species of monocots. We conclude that phylogenetic effects on BCI flowering phenologies are strong within genera, substantially weaker within families, and present but of unknown magnitude within classes.

The strong similarities in overall flowering times among congeners, in the concentration of flowering times among confamilials and in flowering midpoints among monocots came as a surprise. The angiosperms initially radiated in warm, tropical climates (Friis *et al.* 1987; Huntley & Webb 1988), and it seems unlikely to us that these phylogenetic patterns persisted passively throughout their evolutionary history. Alternatively, current adaptive value may continuously reinforce phylogenetic patterns (Harvey & Pagel 1991; Westoby *et al.* 1992). Species that initially shared similar flowering phenologies through descent from a common ancestral species may experience ongoing selection for their common phenology that acts as a brake against the major alterations in genetic, physiological and ecological traits that must accompany any shift to a new phenology.

The flowering phenologies of tropical forest plants are tremendously diverse (e.g. Fig. 1). This diversity has long defied satisfactory explanation in that no general predictive understanding has emerged (for a recent review see Van Schaik *et al.* 1993). Given the strong phylogenetic patterns identified here, we feel that the diversity of tropical flowering phenologies may best be understood within a phylogenetic perspective.

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