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Phenology, Flowering Synchrony, and Fruit Set of Six Neotropical Shrubs¹

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ABSTRACT

Temporal patterns of flower production and the level of fruit set were determined for 20 individuals each of six shrub species (four families) in a semi-deciduous lowland forest in Panama. The species were: *Hybanthus prunifolius*, *Turnera panamensis*, *Rinorea sylvatica*, *Psychotria horizontalis*, *Erythrina costaricensis* var. *panamensis*, and *Pentagonia macrophylla*. There were two objectives of the study: 1) to compare among species the relation between the individual's flowering pattern and the population's flowering synchrony; and 2) to compare within species the relative influence of the individual's and the population's flowering phenology on the individual's fruit set.

The six species differed in number of flowers per individual (mean values for species ranged from 98–2995), how long the individual produced flowers (mean values ranged from 3.5–59.0 days), and synchrony of the individual with its conspecifics (mean values ranged from 0.48–0.95, where value of 1.0 = perfect synchrony). Among the six species, population synchrony increased as the mean duration of an individual's flowering decreased. Population synchrony of the first day, peak (median) day, and the entire flowering period were highly correlated.

When comparing individuals within each species, the individual's flower number was the best predictor of fruit set. Neither the individual's length of flower production nor its synchrony with conspecifics added significantly in explaining the variance in fruit set. A regression including the individual's number of flowers, length of flower production, and synchrony with conspecifics as independent variables and the proportion fruit set (and its arcsin transformation) as the dependent variable yielded no significant regressions.

The consequences of these widely varying phenological patterns are discussed. Comparisons are made with the temporal patterns observed in other tropical forests.

OUR UNDERSTANDING OF TROPICAL REPRODUCTIVE PHENOLOGY is best developed at the community level (flowering: Frankie *et al.* 1974, Putz 1979, Opler *et al.* 1980a; fruit maturation and seed dispersal: Frankie *et al.* 1974, Opler *et al.* 1980a, Foster 1982; germination: Garwood 1983). A few comparative studies are available within one family (Gentry 1974) or one genus (Snow 1965, Stiles 1975). Few phenological studies have focused on the population and the individuals comprising it (Koelmeyer 1959, Bawa 1977, Augspurger 1981, Bullock and Bawa 1981, Bullock *et al.* 1983).

The individual's flowering pattern is defined by the duration of flowering as well as the number and temporal distribution of flowers. Among tropical species, the flowering phenology of individual plants varies continuously between two extreme patterns (Janzen 1971, Heinrich and Raven 1972, Gentry 1974). At one extreme are species with "mass-flowering" individuals producing large numbers of new flowers each day over a week or less. At the opposite extreme are species with "steady-state" individuals producing small numbers of new flowers almost daily for many weeks.

The population's flowering pattern is defined by its component individuals. Variability among individuals in their response to a flowering cue determines the synchrony of the initiation day and consequently affects population

synchrony and flower abundance throughout the population's flowering period. No quantification of population synchrony of flowering is available for tropical species (but see Primack 1980 for temperate measures).

Pollination of an individual's flowers may be influenced by its own pattern of flower production and/or by its synchrony with conspecifics. Previous experimental studies with the tropical shrub, *Hybanthus prunifolius*, demonstrated that mass-flowering by the individual increased attraction of social bees (Augspurger 1980); synchrony with the population further enhanced the individual's seed set (Augspurger 1981).

My study of six shrub species addressed two questions: 1) How does the population flowering synchrony vary among species? *i.e.*, do species with mass-flowering individuals have a higher degree of synchrony than species with steady-state individuals? 2) Within a species, does an individual's fruit set correlate best with aspects of the individual's phenology or those of the population?

Shrubs were chosen because of the ease of quantifying daily flower production and determining fruit set. The species represent large differences in flowering season and duration of flowering. The following six species were studied: *Hybanthus prunifolius* (Schult.) Schulze (Violaceae), *Turnera panamensis* Urban (Turneraceae), *Rinorea sylvatica* (Seem.) O. Kuntze (Violaceae), *Psychotria horizontalis* Sw. (Rubiaceae), *Erythrina costaricensis* Micheli var. *panamensis* (Standl), comb. nov. (Fabaceae), and *Pentagonia macrophylla* Benth. (Rubiaceae).

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TABLE 1. Comparisons of six shrub species of the individual's phenology and pollination level and the population's phenology and spatial pattern. Mean values (\pm 1 standard deviation) are given; N = 20 individuals per population (except N = 10 individuals for fruit set of *Erythrina costaricensis* var. *panamensis*).

	<i>Hybanthus prunifolius</i>	<i>Turnera panamensis</i>	<i>Rinorea sylvatica</i>	<i>Psychotria horizontalis</i>	<i>Erythrina costari- censis</i> var. <i>panamensis</i>	<i>Pentagonia macrophylla</i>
Individual level						
Phenology						
Flowering pattern	Mass- flowering	Mass- flowering	Mass- flowering	Intermediate	Steady- state	Steady- state
Total number of flowers	296 (249)	343 (333)	784 (638)	2995 (3054)	434 (254)	98 (90)
Lifespan of flower (days)	1	1	4	1	1	2
Duration of flower production (days) ^a	4.65 (.99)	7.70 (1.13)	8.10 (.64)	20.15 (3.34)	44.65 (12.05)	58.75 (17.22)
Duration: 90% of flower production (days) ^a	2.35 (.49)	4.60 (.82)	7.05 (.39)	14.55 (2.50)	29.60 (9.88)	49.40 (16.08)
Synchrony with conspecifics ^b	0.89 (.14)	0.77 (.11)	0.95 (.05)	0.82 (.07)	0.50 (.09)	0.48 (.12)
Pollination						
Major visitors of flowers	Social bees	Bees & wasps Butterflies Humming- birds	Bees & wasps	Bees & wasps	Humming- birds	Humming- birds
Number of fruits set	253 (229)	91 (69)	107 (91)	451 (578)	52 (43)	36 (28)
% of flowers setting fruit	82 (13)	31 (16)	14 (8)	13 (9)	15 (10)	33 (28)
Population level						
Phenology						
Duration of flower production (days) ^a	7	12	10	27	80	94
Synchrony of first day ^c	0.77	0.92	0.40	2.22	11.82	16.16
Synchrony of peak (median) day ^d	0.43	1.13	0.60	2.48	11.45	13.59
Synchrony of flowering period ^e	0.89	0.77	0.95	0.82	0.50	0.48
Spatial density	High	Medium-high	High	Medium-high	Low	Low

^a Includes days with no flowers.

^b See Appendix 1A for method of calculation.

^c Calculated as 1 SD around the mean of the first flowering day of 20 individuals; higher values indicate lower synchrony.

^d Calculated as 1 SD around the mean of the peak (median) flowering day of 20 individuals; higher values indicate lower synchrony. For the last three species with no clear peak day (maximum number of flowers), the day the median flower was open was used.

^e See Appendix 1B for method of calculation.

METHODS

The study was conducted in 1976 in the semi-deciduous lowland forest on Barro Colorado Island (BCI), Panama. This well-studied biological preserve is described in detail elsewhere (Leigh *et al.* 1982). Croat (1978) provides descriptions of the six species used in this study.

Before flowering began, 20 individuals of each species were selected. For four species with medium to high density (Table 1), individuals were selected within one hectare; individuals were clumped within each of these species. For two species with low density (Table 1), several hectares were required to locate 20 individuals.

Each individual's flowering phenology was quantified by counting daily the number of newly opened flowers. Individual flowers on one individual of each species were tagged to determine flower lifespan. Summaries of these observations provided daily and total flower production and duration of flowering of each individual.

For comparisons among species two additional values were calculated: 1) the day on which each individual's median flower was open; and 2) the number of days around that median day that encompassed 90 percent of total flower production. Using the 90 percent level of flower production was an arbitrary decision that eliminated the tails of the flowering periods, *i.e.*, days of very

low flower production. All subsequent analyses were restricted to days encompassing 90 percent of flower production.

Flowering synchrony, hereafter referred to as synchrony, was quantified from the perspective of both the individual and the population. Individual synchrony is a composite measure of the amount of overlap of a given individual's flowering days with those of all individuals in the defined population; the method of calculating individual synchrony is presented in Appendix 1A. Population synchrony is a composite measure of the amount of overlap of all flowering days of all individuals with each other individual in the defined population. The method of calculating population synchrony is shown in Appendix 1B; population synchrony equals the mean of the values of individual synchrony as derived from the method in Appendix 1A. The method of measuring population synchrony summarizes the temporal overlap between each set of two individuals in the population from the perspective of both individuals. This measure of population synchrony is a modification of Primack's method (1980), which summarized overlap from the perspective of only one of the two individuals, *viz.* the one with the shortest flowering period. Neither of the synchrony measures takes into account differences among days in the number of open flowers; rather they simply measure overlap on all days an individual has at least one open flower.

Two additional aspects of population synchrony were measured. First, synchrony of the first day of flowering was calculated as one standard deviation around the mean of the first flowering day of 20 individuals. Second, synchrony of the median day of flowering was calculated as one standard deviation around the mean of the median flowering day of 20 individuals. A low standard deviation indicates a high level of synchrony.

Percent of flowers setting fruit and absolute number of fruits set were determined for each of 20 individuals in five species; these measures were limited to ten of 20 individuals in *Erythrina costaricensis* var. *panamensis*. Fruit set measured the pistillate function of the hermaphroditic flowers and indicated that fertilization occurred. This measure was the best estimate of the number of flowers receiving pollen in sufficient quantity to effect fruit set.

Two methods were used to determine fruit set. In Method 1, swollen ovaries were counted directly on the plant. Ovaries of some species are known to swell slightly without pollination. Therefore, experiments were also carried out on flowers emasculated and bagged to prevent pollination. A comparison of their ovary size with that of flowers artificially pollinated indicated the minimum size of ovary required to indicate that pollination had occurred. This direct method of determining fruit set was applied to individually tagged flowers of *Hybanthus prunifolius* and *Rinorea sylvatica*, five days after each flower's functional lifespan, and to *Pentagonia macrophylla* and

Psychotria horizontalis, eight and nine weeks after flowering, respectively; neither of the latter two species provided early indication of pollination.

In Method 2, applied to *Turnera panamensis* and *Erythrina costaricensis* var. *panamensis*, aborted ovaries on the ground were counted daily and removed. These species had been experimentally shown to consistently abort non-pollinated flowers, but not pollinated flowers, two days after each flower's functional 1-day lifespan. By subtracting number of freshly aborted ovaries from number of open flowers two days prior to ground collection, an indirect estimate was obtained of the number of non-aborted, and assumed pollinated, ovaries remaining on the plant. *T. panamensis* and *E. costaricensis* var. *panamensis* are tall shrubs; thus Method 2 was considered superior to a direct count of swollen ovaries from the vantage point of the ground.

Measurements of fruit set occurred either two or five days after the flower was open in *Hybanthus prunifolius*, *Rinorea sylvatica*, *Turnera panamensis*, and *Erythrina costaricensis* var. *panamensis*. By that day, all flowers experimentally excluded from pollinators had aborted, while all experimentally pollinated ovaries remained on the plant. Counts made so quickly after flowering were likely to indicate only whether or not pollen was received by the flower; abortion of experimentally pollinated ovaries, due to unknown causes such as predation or resource limits, occurred only after this period. In *Pentagonia macrophylla* and *Psychotria horizontalis*, measurements of fruit set were made weeks after pollination. Therefore, their fruit set could not be used to indicate pollination only, as selective abortion and predation of pollinated ovaries may have occurred prior to measuring fruit set.

The timing and method of determining fruit set, and what fruit set represented, differed among the six species. Therefore, interspecific comparisons of fruit set were unwarranted; only intraspecific comparisons of fruit set were made.

RESULTS

Phenology varied widely among the six species at both the individual and population levels (Fig. 1, Table 1). The lifespan of a flower varied from 1–4 days among the species (Table 1). The total number of flowers per individual did not differ significantly among five of the six species (Tables 1 and 2). However, the six species varied significantly in how long the individual produced those flowers (Tables 1 and 2). The six species represented three phenological patterns. Three species had “mass-flowering” individuals; their day of median flower production coincided with the day of peak flower production. Two species had “steady-state” individuals with no marked peak of flower production; individuals had similar numbers of flowers for many days before and after the day on

TABLE 2. Comparisons of the individual's phenological variables among the six species. Underlined values indicate means not significantly different ($P < .05$) by Student-Newman-Kuels Multiple Range test. Abbreviations refer to first letter of genus and species of each species. Species are arranged in order from lowest (left) to highest values.

Variable	Analysis of variance			Student-Newman-Kuels Multiple Range test					
	<i>F</i>	<i>df</i>	Signif.	<u>Pm</u>	<u>Hp</u>	<u>Tp</u>	<u>Ec</u>	<u>Rs</u>	<u>Ph</u>
Total number of flowers	14.19	5, 114	$P < .0005$	<u>Pm</u>	<u>Hp</u>	<u>Tp</u>	<u>Ec</u>	<u>Rs</u>	<u>Ph</u>
Duration: 90% of flowers	110.70	5, 114	$P < .0005$	<u>Hp</u>	<u>Tp</u>	<u>Rs</u>	<u>Ph</u>	<u>Ec</u>	<u>Pm</u>
Synchrony with conspecifics ^a	79.54	5, 114	$P < .0005$	<u>Pm</u>	<u>Ec</u>	<u>Tp</u>	<u>Ph</u>	<u>Hp</u>	<u>Rs</u>

^a See Appendix 1A for method of calculation.

which the median flower was produced. One species had individuals with an intermediate pattern. Finally, the six species varied significantly in the individual's synchrony with conspecifics (Tables 1 and 2; Fig. 1). The six species fell into three categories: those with a high, medium, and low degree of synchrony (Tables 1 and 2).

Among the species the mean flower number was not significantly correlated with the mean duration of flowering or population synchrony (Table 3). All other phenological characters were significantly correlated (Table 3; Fig. 1). Mean duration of individual flower production significantly correlated with population synchrony of the first and peak (median) days of flowering and of the entire flowering period; species with shorter individual flowering periods had a higher degree of synchrony. For species that initiated flowering more synchronously, peak (median) flowering also tended to occur more synchronously. Finally, a high degree of synchrony for the entire flowering period resulted among species with a high degree of synchrony for first and peak (median) days of flowering.

To evaluate the relative influence of the individual's and the population's phenology on the individual's pollination, a multiple regression analysis was performed for each species. In the first set of analyses, number of fruits set was the dependent variable and flower number, 90 percent duration of flowering, and individual synchrony were the independent variables. When the population variable (synchrony) and both the individual variables (flower number and duration) were all included, the regression was clearly significant for *Hybanthus prunifolius*, *Turnera panamensis*, *Rinorea sylvatica*, *Psychotria horizontalis*, and *Pentagonia macrophylla* ($P < 0.05$). It was not significant for *Erythrina costaricensis* var. *panamensis*; in measuring fruit set in this species, $N = 10$ individuals, while in all other species, $N = 20$ individuals.

Next, when synchrony was eliminated, the regression was still significant and there was no significant reduction in the variance explained by the regression. When duration of flowering was eliminated, the regression was still significant and again there was no significant reduction in the variance explained by the regression. Simple correla-

tion analysis revealed that the number of flowers, but not the duration of flowering, was significantly correlated with the number of fruits set in five of the six species (Table 4). Thus these analyses reveal that one variable alone, the individual's flower number, was the best predictor of number of fruits set in all species, except *Erythrina costaricensis* var. *panamensis*. Variation in the individual's phenology, and not in the population's phenology, explained the variation in the individual's pollination.

Identical analyses as above were performed for each species, using first, the proportion of flowers setting fruit, and second, the arcsin transformation of proportion fruit set as the dependent variable. These analyses yielded no significant regressions. Furthermore, simple correlation analyses, in general, showed no significant relationships (Table 4). Only *Turnera panamensis* showed a negative relation between both the individual's number of flowers and its synchrony with conspecifics with the proportion of its flowers setting fruit (Table 4). Also, in three of six species, individuals with longer flowering periods had less synchrony with conspecifics (Table 4).

DISCUSSION

Clear phenological patterns emerged when detailed quantitative studies at the individual and population levels were undertaken. The six shrub species of this study differed in three major components of the individual's phenology: number of flowers, duration of flowering, and synchrony with conspecifics. In the discussion I consider possible consequences of and explanations for such patterns, and where possible, make comparisons with the patterns in other tropical forests.

Historically, research in phenology has been lacking in two respects: quantification of phenological patterns and precise use of clearly defined descriptive terms. Consequently, adequate descriptions of temporal patterns of flowering are lacking for most tropical species. The timing of the individual and the population are often not discriminated. For example, "gregarious" is frequently used to imply "synchronous," especially if the flowering period

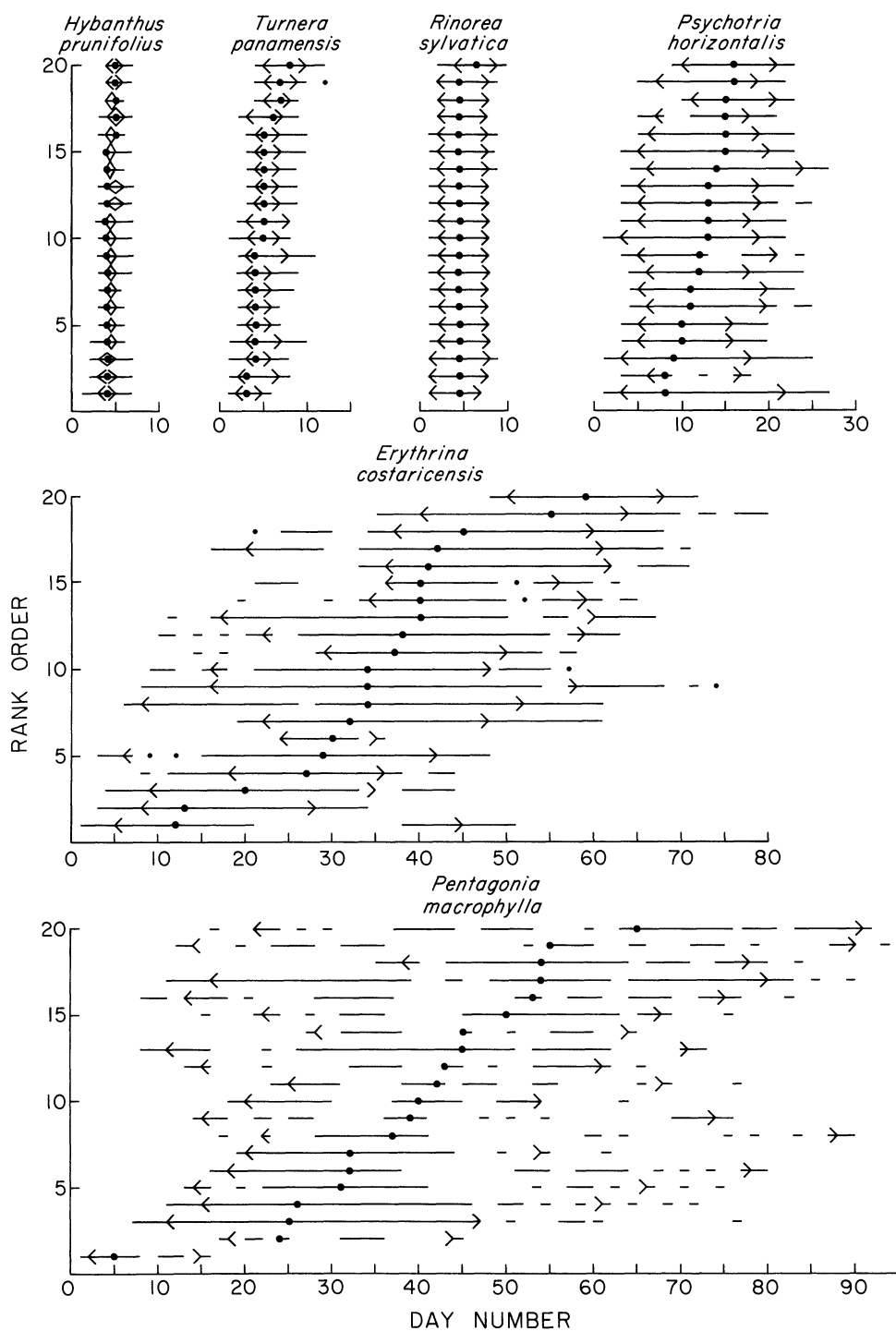


FIGURE 1. Timing of flowering of individuals arranged in rank order of the day the median flower was open ($N = 20$ for each of six species). Each horizontal line represents the total duration of flowering by an individual. A broken line indicates discontinuous flower production. The brackets enclose the period around the median flower day during which 90% of an individual's flowers were open. The heavy dot indicates the day the median flower was open; this day corresponds to the peak day (maximum number of flowers) for mass-flowering individuals of the first three species.

TABLE 3. Pearson correlation coefficients for phenological characters of the six species. Analyses are at the population level; N = six species. Correlation coefficients were calculated from Table 1 using mean values for number of flowers and duration of flower production under individual level and values for synchrony under population level.

	Total number of flowers	Duration: 90% of flowers	Population synchrony of first day	Population synchrony of peak day	Population synchrony of flower period
Total number of flowers	—				
Duration: 90% of flowers	-.198	—			
Population synchrony of first day ^a	-.334	.976***	—		
Population synchrony of peak day ^a	-.302	.964**	.995***	—	
Population synchrony of flowering period ^b	.328	-.891*	-.949***	-.962***	—

^a Calculated as 1 SD around the mean.

^b See Appendix 1B for method of calculation.

^c The correlation is negative because of differences in the methods used to calculate synchrony values. For synchrony of first and peak days, a low standard deviation indicates a high degree of synchrony. In contrast, for synchrony of the entire flowering period, high values indicate high synchrony.

* $P < .05$, ** $P < .005$, *** $P < .0005$.

is short (Holtum 1935, Longman and Jenik 1974). With that definition, it is unclear whether the short flowering period refers to the individual and/or the population. Only when population synchrony is perfect are the durations of the individual and the population periods equivalent.

Baker (1959) suggested from qualitative observations that asynchronous flowering of the population is common

in the tropics. Quantitative data to test that generalization have been lacking. Frankie *et al.* (1974) listed 13 percent of tree species in the wet lowland rainforest of Costa Rica as “unsynchronized” in their population flowering, but “unsynchronized” was not defined in that study. The quantitative data from the present study indicated that the shrub species fell along a continuum of population synchrony. All were synchronous to a degree; they simply

TABLE 4. Pearson correlation coefficients for various phenological characters and percent fruit set and number of fruits set. Analyses are at the individual level for each species; N = 20 individuals, except N = 10 individuals for fruit set of *Erythrina costaricensis* var. *panamensis*.

Variables	<i>Hybanthus prunifolius</i>	<i>Turnera panamensis</i>	<i>Rinorea sylvatica</i>	<i>Psychotria horizontalis</i>	<i>Erythrina costaricensis</i> var. <i>panamensis</i>	<i>Pentagonia macrophylla</i>
Total number of flowers—						
% fruit set	.207	-.454*	-.054	.263	-.128	-.149
Duration: 90% of flowers—						
% fruit set	.290	.207	.043	.194	.135	.197
Synchrony with conspecifics ^a —						
% fruit set	-.283	-.472*	.096	.146	.368	.313
Total number of flowers—						
total number of fruit	.991***	.708**	.652**	.875***	.513	.510*
Duration: 90% of flowers—						
total number of fruit	.344	-.268	.167	.241	.401	.295
Synchrony with conspecifics ^a —						
total number of fruit	-.393	.396	.089	.081	-.152	.240
Total number of flowers—						
duration: 90% of flowers	.325	-.209	.335	.440	.398	.247
Total number of flowers—						
synchrony with conspecifics ^a	-.376	.383	-.210	-.115	-.072	.031
Duration: 90% of flowers—						
synchrony with conspecifics ^a	-.994***	-.629**	-.108	-.732**	-.090	.134

^a See Appendix 1A for method of calculating individual synchrony.

* $P < .05$, ** $P < .005$, *** $P < .0005$.

varied in the extent of their synchrony. This result implies that the dichotomy "synchronous" versus "asynchronous" may not always be appropriate.

The mean number of flowers per individual did not differ significantly among five of the six species; a high variation in flower number occurred among individuals within each species, however. Species with mass-flowering and steady-state individuals had roughly equivalent numbers of flowers. Therefore, the major difference in their phenological pattern was in the duration of flowering and flower production per day.

Mean duration of the individual's flowering period ranged among the six species from 4.6–58.8 days (2–49 days for 90% of flower production). Short flowering periods occurred in the dry season, long ones in the wet season. The only extensive community study of the phenology of tropical shrubs and treelets occurred in dry and wet forests of Costa Rica (Opler *et al.* 1980a). In that study, individuals in tree species in the dry forest produced flowers for shorter periods (mean = 7.9 weeks) than did individuals in treelet and shrub species (mean = 11.7 weeks). The blooming period varied by habitat, however; shrubs in the dry hill forest had an individual average of 4.7 weeks, while those in dry secondary forest flowered for 19.8 weeks. Opler *et al.* (1980b) noted that early successional species generally have more extended flower periods than those in mature communities. Continuous and extended flower production by treelet and shrub individuals was greater in wet forest (28% of the species) and riparian forest (30%) than in dry hill forest (17%) (Opler *et al.* 1980a). In a more aseasonal forest in Malaysia, Putz (1979) noted that 66 percent of species flowered neither for long periods nor at regular intervals; the duration of flowering was highly variable within a tree species.

Bawa (1983) outlined possible selective forces affecting the length of the individual's flowering period. Of particular importance are: regulation of pollen flow, foraging behavior of pollinators, rate of fruit development in response to resource availability, and habitat (as observed above). The length may also be affected by the availability of an environmental cue to synchronize an individual's flowering with conspecifics (see below).

The short period of mass-flowering individuals may be a response to competition for pollinators: their super-abundant resources are thought to attract many types of opportunistic pollinators with density-dependent foraging behaviors (Janzen 1967, Heinrich and Raven 1972, Gentry 1974, Frankie *et al.* 1976). My observations showed that many different foraging species visited each of the three species with mass-flowering individuals. However, a more thorough study of *Hybanthus prunifolius* showed that most of the 22 species of visitors were ineffectual pollinators and that one social bee effected most fruit set

(Augspurger 1980). Hence, attraction and pollination are not necessarily equivalent for these species.

The abundant resource used to attract pollinators to mass-flowering individuals has the potential to produce low inter-plant movement. This would result in low out-crossing, particularly for self-compatible species (*e.g.*, *Hybanthus prunifolius*, see Augspurger 1980), or in low percentage fruit set for self-incompatible species (*e.g.*, *Turnera panamensis* is heterostylous and self-incompatible; personal observation). In *Hybanthus prunifolius* detailed observations indicated that bees visited only about 5 percent of available flowers on an individual and then moved, frequently to other conspecifics (Augspurger 1980). Inter-plant movement between mass-flowering trees has also been observed (Frankie *et al.* 1976). This movement may be promoted by several factors: aggressive interactions among pollinators (Frankie *et al.* 1976, Rausher and Fowler 1979), presence of toxic compounds in nectar (Rhoades and Bergdahl 1981), or variability among individuals in timing, amount, and composition of nectar secretions (Frankie and Haber 1983). Bees continually monitor changing resource levels; detection of these changes apparently prompts large bee pollinators to make inter-tree movements, thereby effecting cross-pollination.

Mass-flowering may also lower flower predation (Bawa 1983) or, in later reproductive stages, seed predation (Augspurger 1981). The short flowering period may impose some risk if it occurs during unfavorable weather conditions for pollination or for subsequent reproductive stages. The short flowering by individuals of *Hybanthus prunifolius* was followed in one year by an extreme dry period when many of the rapidly developed fruits aborted due to drought (Augspurger 1978).

In contrast to mass-flowering, other species had individuals with steady-state flowering producing a few flowers regularly for many days. They were visited by a low diversity of hummingbird species, predominantly non-territorial foragers, although some territoriality was observed at large individuals of *Erythrina costaricensis* var. *panamensis*. This group of pollinators are known to regularly visit widely spaced individual plants (Stiles 1975). The individual's low flower production per day promotes cross-pollination and perhaps increases the number of different individuals with which a plant mates. The latter depends on the regularity of the pollinator's foraging path. Extended flowering lessens the risk of flowering during sporadic bad weather (Bawa 1983). It may also allow the regulation of the relative number of flowers versus fruits in response to changing availability of resources (Lloyd 1980).

The six shrub species ranged in the population synchrony from .48–.95 on a scale of 0–1. The population synchrony of the first day, peak (median) day, and the

entire flowering period were highly correlated. This suggests that variability among individuals in their initial response to the flowering cue subsequently affects synchrony throughout the flowering period. In three temperate shrubs synchrony varied from .34–.74 (Primack 1980) (but note differences between this study and Primack's in method of quantifying synchrony; see methods and Appendix 1). Putz (1979) noted that about 50 percent of Malaysian tree species lacked intra-population synchrony. Opler *et al.* (1980a) observed that in the wet forest of Costa Rica, population asynchrony was more common in shrubs and treelets (33% of species) than in trees (13%). In the wet forest, in general, synchrony was not always marked. In the dry forest, slightly more of the "brief" (less than 2 weeks per individual) species were synchronous (85%) than the extended (greater than 2 weeks) species (79%). Frankie *et al.* (1974) found that species of trees were more synchronous in the dry than in the wet forest.

In the current study, high values of population synchrony were associated consistently with four variables. First, population synchrony increased among species as the mean individual flowering duration decreased. Species with mass-flowering individuals had nearly twice as high synchrony values as species with steady-state individuals. This quantitative conclusion confirmed many earlier qualitative observations. Species with mass-flowering individuals were commonly observed to have high population synchrony (Müller 1882, Schimper 1903, Spruce 1908, Coster 1926, Kerling 1941, Janzen 1967, Opler *et al.* 1976).

Second, high population synchrony was associated with high population density. Thus, *Hybanthus prunifolius*, *Turnera panamensis*, and *Rinorea sylvatica* had a very high, but ephemeral flower density in the forest as a whole. This flower density accrued from the flowering pattern of both the individual and the population, and from the spatial distribution of the population.

Third, the species with high ephemeral flower density also shared a common and unambiguous flowering cue. The species with mass-flowering individuals all flowered in the dry season, a few days after a heavy rain caused sudden and large changes in soil moisture. The specific cue requirements have been identified experimentally for *Hybanthus prunifolius*. That shrub requires first a drought of 1–2 months, after which it flowers rapidly after sudden changes in soil moisture associated with rainfall (Augsburger 1982). Similarly, aseasonal showers during the dry season in Costa Rica have been shown to correlate with the onset of anthesis by several species with short, highly synchronized flowering (Opler *et al.* 1976). Poore (1968) and Medway (1972) also observed the importance of external cues in affecting synchrony in the more aseasonal tropical forests of the Old World; gregarious

flowering occurred in response to drought. Corner (1952) and Holttum (1953) suggested it was associated with a decrease in temperature accompanying storms.

Fourth, population synchrony was also enhanced by the production of well-developed preformed flower buds that go dormant and await a flowering cue (Rutgers and Went 1915, Seifrizz 1923). The time from cue to flowering was quite short, thus leading to low variability among individuals in developmental rates and high population synchrony. *Hybanthus prunifolius* and *Rinorea sylvatica* formed preformed flower buds; *Turnera panamensis* appeared to do so facultatively. The bud of *Rinorea sylvatica* most closely approached the size of its open flower; that species had the highest population synchrony of the six species.

The two species with low population synchrony, *Erythrina costaricensis* var. *panamensis* and *Pentagonia macrophylla*, shared common features that are opposite the above three species. Their individuals exhibited a steady-state flowering phenology in response to an unknown cue in the wet season. They did not form well-developed, dormant flower buds and they occurred in quite low density. Similar asynchrony of flowering, as well as leaf fall and shoot emergence, was observed in populations of *Erythrina peoppigiana* in Costa Rica (Borchert 1980); an increase in its flowering synchrony occurred with increasing drought.

Finally, the sixth species, *Psychotria horizontalis*, shared features with both groups of species. This species may flower in the late dry or early wet season or both following heavy rains. It facultatively made preformed flower buds in response to weak rains in the dry season. The population's flowering synchrony was fairly high, but its daily flower production was relatively low and was spread over an intermediate length of time.

Several hypotheses exist to explain selection for a high degree of synchrony with conspecifics: 1) increase in the potential for cross-pollination, a requirement if the individual is self-incompatible (Holttum 1953, 1954; Baker 1959; Bawa 1983); increase in the efficiency of energetics of pollinators (Heinrich and Raven 1972); attraction of pollinators (Corner 1952, Beattie *et al.* 1973, Gentry 1974, Opler *et al.* 1976, Bawa 1983); and escape from flower and later seed predators (Beattie *et al.* 1973). Experimental tests of these hypotheses are limited to the last two. In *Hybanthus prunifolius*, both pollinator attraction and seed predator avoidance were enhanced in a naturally synchronous population relative to an experimentally-induced asynchronous population (Augsburger 1981).

Selection for synchrony has apparently been less strong within species with individuals with steady-state flowering. For long-flowering individuals, being out of phase by a few days with conspecifics, especially those at some

distance in these rare species, may have little consequence for cross-pollination and fruit set, relative to a mass-flowing individual. In the latter group, being asynchronous to the same degree would have a major effect, greatly lowering the population density at which it flowered and the number of nearby individuals with which it could mate. Extremely high densities of flowers at one time can not be achieved by a population of steady-state individuals. In these species, the individual by itself is not using high density to attract a density-dependent pollinator. Furthermore, little density effect is gained from overlapping in time precisely with the population.

It is impossible to know today the order in which a species' characteristics became linked in the past. Selection on bud formation, season of flowering, type of flowering cue, length of flowering, pattern of flower production, and synchrony with conspecifics is likely to be closely intertwined. The differences in synchrony among the species may be due simply to selection on bud formation, the flowering cue, and season of flowering. These factors relate directly to the mechanism an individual uses to time its flowering; indirectly they affect its synchrony with conspecifics. Alternatively, selection directly on the individual's synchrony, due to pollinator attraction and movement and the importance of cross-pollination, may vary among the species and explain the observed variation in population synchrony. These evolutionary factors directly regulate population synchrony by differentially affecting the reproductive fitness of its component individuals. Borchert (1983) argued that the evolution of phenolog-

ical patterns of tropical trees is not the result of biotic factors alone, but is also influenced by tree architecture and vegetative, bud, and flower development.

Within a species, variance in only one aspect of the individual's phenology, flower number, was useful in explaining the variance among individuals in the number of fruits set. Duration of flowering and synchrony with conspecifics were not significant variables. The proportion of fruit set by the individual was not significantly affected by any of the three variables. These results do not indicate that duration and synchrony *per se* are of no importance to the individual. Rather, they illustrate that, at the existing level of variation among individuals in the population, in conjunction with all other variables affecting fruit set, they are not predictive of levels of fruit set. To test directly the effect of synchrony on the individual's fruit set requires experimental manipulation of the individual's flowering time away from that of conspecifics. At such extremes in variation in timing, the importance of synchrony may be more readily detected, as was demonstrated in the earlier studies of *Hybanthus prunifolius* (Augsburger 1981).

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APPENDIX 1. Methods of Calculating Synchrony (modified from Primack 1980).

A. Synchrony of a given individual with its conspecifics:

X_i , the index of synchrony for individual i , is defined as:

$$X_i = \left(\frac{1}{n-1} \right) \left(\frac{1}{f_i} \right) \sum_{j=1}^n e_{ij}$$

where, e_{ij} = number of days both individuals i and j are flowering synchronously, $j \neq i$;

f_i = number of days individual i is flowering;

n = number of individuals in population.

When $X = 1.0$, perfect synchrony occurs, *i.e.*, all flowering days of individual i overlap with all flowering days of each other individual, $j \neq i$, in the population.
When $X = 0.0$, no synchrony occurs, *i.e.*, no overlap occurs among any of the flowering days of individual i and any other individual, $j \neq i$, in the population.

B. Synchrony of the population:

Z , the index of population synchrony, is defined as:

$$Z = \frac{1}{n} \sum_{i=1}^n X_i$$

where X_i is synchrony of individual i with its conspecifics from part A (above).