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Flowering Synchrony of Neotropical Plants

Carol K. Augspurger

El sincronismo en la floración es importante para las especies tropicales y afecta el éxito reproductivo y la estructura de la población. La selección en relación al sincronismo puede actuar sobre el individuo a través de un número de mecanismos y el grado de sincronización varía con el estado reproductivo. El éxito del individuo es parcialmente determinado por su sincronización con el resto de su población.

Patterns of Flowering Synchrony

Early biologists visiting the tropics noted the highly "gregarious" (synchronous) flowering of certain species, especially those with individuals in flower for a very short time (Mueller 1882, Schimper 1903, Spruce 1908, Coster 1926, Holttum 1935). Spruce (1908) said of the Amazonian Myrtaceae: "They are remarkable for their simultaneous and ephemeral flowers. On a given day all the myrtles of a certain species, scattered throughout the forest, will be clad with showy fragrant flowers; on the following day nothing of flowers appears save withered remnants." Another well-documented example of synchronous flowering occurs in the pigeon orchid *Dendrobium crumenatum* that flowers for only 1–2 days but synchronously over a wide geographic area in the Far East (Holttum 1949, 1954).

On the other hand, Baker (1959) suggested that asynchronous flowering is common in the tropics and that the proportion of neighboring trees of the same species in flower at the same time may be extremely low. The first phenological study to provide systematic observations of synchrony for many different tropical species took place in Costa Rica where asynchrony occurred in 13% of the tree species and in 33% of the treelet and shrub species in a wet forest, and in 2% of the tree species in a dry forest (Frankie et al. 1974, Opler et al. 1980). A species with only infrequent deviants was not designated as asynchronous, and the category of asynchrony appears to have

been assigned only if some individuals flowered at a completely different time than other members of the species. The sample size per species was small (2.5 individuals at wet site, 10.2 at dry site).

A more quantitative study indicated that synchrony is not a dichotomy—asynchronous versus synchronous—but rather is a continuum when comparisons are made among various species in a community (Augspurger 1983). There daily flower production was quantified for 20 individuals for each of 6 shrub species on Barro Colorado Island (BCI) (Fig. 1). The 6 species differed greatly in the mean length of an individual's flowering period and the mean number of flowers per individual (Table 1).

La sincronización en la floración ha sido señalada por varios científicos, sin embargo en muchas especies la floración es asincrónica. En la floración en los trópicos hay un patrón continuo entre sincronismo y asincronismo.

Synchrony of the day of onset of flowering was quantified as the standard deviation among 20 individuals. A decrease in the value of the standard deviation indicated greater synchrony. Peak day of flowering was not chosen for comparison because individuals in the 3 species with long flowering times did not have a readily defined peak day; their flower production was distributed evenly over time.

Synchrony of the onset of flowering increased as the mean length of flowering per individual decreased (Table 1). The day of onset of flowering was more

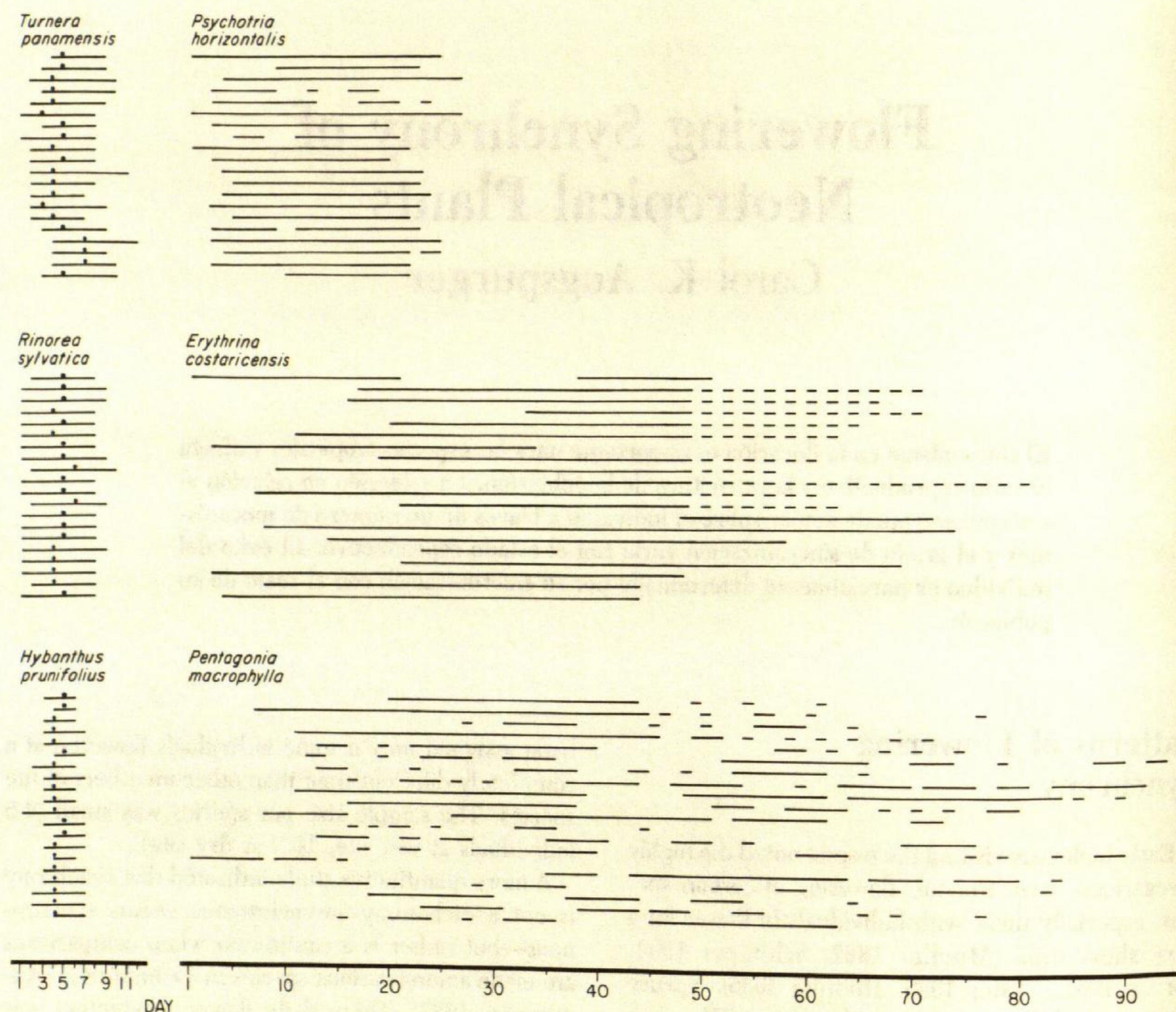


Fig. 1. Comparisons among 6 shrub species of timing of flowering of 20 individuals per species. Each line represents length of time an individual is in flower. Dot above line represents day with largest number of flowers (peak day). Flower number per day for the 3 species with longer flowering periods was fairly constant; therefore no peak day is noted for those species. A dotted line for *Erythrina costaricensis* equals period of estimation; only final day of flowering is known with certainty for those individuals.

TABLE 1
PHENOLOGICAL AND POLLINATION CHARACTERISTICS OF SIX SHRUB SPECIES DEPICTED IN FIGURE 1

	Hybanthus prunifolius	Turnera panamensis	Rinorea sylvatica	Psychotria horizontalis	Erythrina costaricensis	Pentagonia macrophylla
Mean no. of flowers per individual	226	499	802	2816	344	64
Mean no. of days per individual	3.7	7.3	8.1	21.0	44.0	59.0
Synchrony of onset of flowering ¹	1.02	0.97	0.31	2.14	11.82	16.16
Season of flowering	Dry	Dry	Dry	Dry-Wet	Wet	Wet
Compatibility and pollination system	Self-Comp. Needs Vistation	Incomp. Heterostyly	?	Incomp. Heterostyly	Incomp.	?
Pollinator	Social bee	Mixture	?	Small bees & wasps	Hummingbird	Hummingbird
Spacial density	High	Medium	High	Medium	Low	Low

¹Synchrony calculated as 1 standard deviation around the mean day of onset for 20 individuals of each species.

synchronous in species with individuals that flower for a short time than in species with individuals that flower for a long time. Minor variability in synchrony occurred among populations of the same species at different sites and in different years (Table 2).

Importance of Flowering Synchrony

Flowering synchrony has important implications for both the individual plant and the population. For the individual, synchrony can affect both the quantity and the genetic qualities of its offspring. Flowering synchrony is a requirement for successful reproduction by an obligatory outbreeding individual—dioecious or self-incompatible. Synchrony can also influence the amount of outbreeding of a self-compatible individual and the number of mates with which it may breed.

Synchrony may therefore also influence mate selection if the female can differentially abort ovules on the basis of the genetic qualities of the male. As such, synchrony may influence the genetic quality of offspring of an individual.

Synchrony may also influence the quantity of offspring produced in one season and over an individual's lifetime. If synchrony with the population increases the ability of the individual to attract pollinators (see later), a synchronous individual may begin to reproduce at a smaller size or earlier age than an

asynchronous individual. Synchrony then also influences the number of offspring produced in all subsequent reproductive episodes. The timing of flowering may also influence the individual's synchrony during its subsequent reproductive stages, such as fruit and ovule maturation, seed dispersal, and germination (see later).

Flowering synchrony influences the genetic structure of the population and delimits its effective size (Wright 1946). By defining the number of individuals with potential to exchange genes, synchrony can affect the probability of genetic drift and gene fixation and influence local differentiation of populations and the rate of evolution.

La sincronización de la floración puede influir en la calidad genética de la descendencia al igual que en la cantidad de descendencia. Igualmente, influye en la sincronización de etapas subsiguientes, tales como la maduración de frutos y óvulos, dispersión y germinación de semillas.

At first glance it might appear that the less synchronous species (Table 1) have less potential for exchange of genes among individuals (i.e., for gene flow). However, synchrony in this analysis was quantified only for the day of onset of flowering and not for the entire flowering period. Even though species with long individual flowering periods are less synchronous in the day of onset, nevertheless each individual has a long overlap with other individuals when the entire flowering period is considered (Fig. 1). In contrast, in a species with a short flowering period, one day's deviation by an individual in the onset of its flowering results in a large loss of overlap over its flowering period (Fig. 1). The major conclusion is that species differing greatly in synchrony of onset of flowering may actually have quite similar overlap when the entire lengths of their flowering periods are considered. Selection for time of onset of flowering must be greatest in species with individuals with short flowering periods so there is overlap throughout the individual's flowering period. Until a better method of quantifying overlap throughout the flowering period is developed, the role of timing of flowering in influencing gene flow in a population cannot be accurately determined. The type of breeding system must also be considered in evaluating the potential for gene flow.

La sincronización del principio de la floración es mayor en especies con períodos de floración cortos.

TABLE 2
VARIABILITY OF SYNCHRONY IN FLOWERING AND
SEED DISPERSAL BETWEEN SITES AND
YEARS FOR *HYBANTHUS PRUNIFOLIUS*

	Synchrony of Onset ¹			
	1975	N	1976 ²	N
Flowering				
Site 1	1.69	10	0.56	16
Site 2	1.53	20	0.85	20
Site 3	1.18	20	0.91	20
Site 4	1.02	20	0.43	20
Mean	1.36		0.69	
Seed Dispersal³				
Site 3	3.01	20		

¹Synchrony calculated as 1 standard deviation around the mean day of onset at each site.

²The rain triggering flower anthesis was much heavier in 1976 than in 1975.

³Synchrony of onset of seed dispersal is significantly lower than onset of flowering at this site ($F = 6.52$, p less than .0005).

Evolutionary Factors Influencing Synchrony

Ultimate (evolutionary) factors are those affecting the reproductive fitness of the individual. They explain the evolutionary basis for the timing of flowering of the individual plant. The most frequently mentioned hypothesis to explain the evolution of flowering synchrony is that it increases potential for out-crossing (Holttum 1954, Moore & Lewis 1965, Whitehead 1969, Stern & Roche 1974, Opler et al. 1976). This hypothesis has never been directly tested. Greater outcrossing is a possible result of synchrony, but outcrossing need not be a determining selective factor.

Alternative and supplementary hypotheses involving biotic factors leading to reproductive synchrony include 1) minimization of hybridization and pollen wastage (isolating mechanism) (Smith 1926, Grant 1949), 2) increasing foraging efficiency of pollinators that are (more) likely to remain constant to one species of plant (Heinrich & Raven 1972), 3) increasing pollinator attraction (Corner 1940, Beattie et al. 1973, Opler et al. 1976), and 4) lowering herbivory (predation) of an individual's seeds and fruits by the population satiating the herbivores (Smith 1970, Janzen 1971, Beattie et al. 1973). The last hypothesis is most relevant for those species attacked by herbivores during or shortly after the flowering stage when synchrony is still unchanged and for species with fruiting synchrony comparable to flowering synchrony (see later).

Se considera que la sincronización de la floración incrementa el cruzamiento, minimiza la hibridación y el desperdicio de polen, aumenta la eficacia de los polinizadores y la atracción a éstos, además de que disminuye la destrucción de semillas por herbívoros.

Limits to effectiveness of synchrony may occur if the amount of flowers produced becomes too large for the local pollinators to service. Pollinator satiation may then be a factor affecting the degree of synchrony among tropical trees with their massive floral displays.

These evolutionary arguments require a genetic basis to timing among individuals in a population. Numerous temperate studies indicate that timing of flowering is heritable (McMillan & Pagel 1958, Cooper 1960, Paterniani 1969, Harris 1970, Stern & Roche 1974, Hodgkin & Quinn 1978). In some species early-versus late-flowering of individuals can be explained

by a single gene (McIntyre & Best 1978). Selection on variation of timing of a population can greatly affect synchrony of flowering in only a few generations (McNeilly & Antonovics 1968, Paterniani 1969). These genetic studies do not directly indicate which of the proximate factors that control timing of flowering are affected by selection. Data for non-domesticated tropical species on the genetics and timing of flowering are not yet available.

La sincronización de la floración podría ser heredada por mecanismos simples.

Ecological Factors Influencing Synchrony

Evolutionary factors explain why synchrony is advantageous to an individual, but how is such synchrony achieved by the individual? Proximate (ecological) factors relate to the mechanism an individual uses to ensure it flowers synchronously with its conspecifics. Selection can act on several aspects of the timing of an individual: 1) preparation for the flowering response, 2) nature of the environmental trigger initiating the response, and 3) the developmental changes involved in the response itself.

El proceso de selección de la sincronización puede actuar sobre el individuo mediante la preparación para florecer, mediante factores ambientales que inician la respuesta y a través de pasos de desarrollo asociados con la respuesta.

First, the preparation for the flowering response includes the induction of flower buds. Bud initiation may be followed by continuous development to flower anthesis, or it may be followed by a period of dormancy at some incomplete stage of development. Additional factors are then required to break dormancy and to complete development and flower anthesis.

Other things being equal, less variation in timing of flowering is expected if dormant buds are formed, especially if dormancy begins at a late stage of bud development. Then when the environmental trigger for anthesis occurs, less variation in development timing occurs and higher synchrony results.

In a phenological study of the shrub species, *Psychotria horizontalis* (Rubiaceae), on BCI, flowering synchrony was higher in a population that experienced bud dormancy than in one with no bud dormancy (Table 3). Normally this species responds to heavy rains, usually at the beginning of the wet

TABLE 3
ONSET OF FLOWERING SYNCHRONY IN
PSYCHOTRIA HORIZONTALIS CHANGES WITH
DORMANT BUDS PREFORMED PRIOR TO RAINS

	Onset of First Flowering		Onset of Second Flowering		
	Synchrony ¹	Range ²	Synchrony	Range	n
Site 1 ³	3.09	13	1.00 ⁴	5	20
Site 2 ⁵	2.22	10	4.93	24	20

¹Synchrony calculated as 1 standard deviation around the mean day of onset at each site.

²Number of days encompassing the onset day of all individuals at the site.

³Plants at this site responded to the first heavy rain by forming flower buds; anthesis occurred in a few buds in all plants. Anthesis of most of these preformed buds occurred with the second rain.

⁴Synchrony of second flowering at Site 1 (with preformed buds) was greater than first flowering of either Site 1 (no preformed buds) ($F = 9.55$, p less than .0005) or Site 2 (no preformed buds) ($F = 4.93$, p less than .0005).

⁵Plants at this site responded to the first heavy rain by forming flower buds; anthesis of all buds immediately followed. A few new flower buds were formed with the second rain.

season, by undergoing an uninterrupted developmental sequence from bud induction through flower anthesis. However, in one year in one population on the plateau of the island, a heavy rain late in the dry season induced bud development, but not much flower anthesis. A second heavy rain at the beginning of the wet season was followed by highly synchronous flowering in that one population. Other populations on other areas of the island flowered after the first rain, but with less synchrony.

La formación de yemas latentes permite mayor sincronización de la floración. En la IBC, *Psychotria horizontalis* presentó mayor sincronización en poblaciones que poseen yemas latentes. Esta especie normalmente manifiesta desarrollo ininterrumpido desde las yemas hasta las flores en respuesta a las lluvias fuertes.

Rutgers and Went (1915) and Seifriz (1923) noted that tropical plants with high synchrony form dormant buds. In the study on BCI, the three species with the highest synchrony form dormant buds; the three with the lowest synchrony do not normally do so (Augspurger 1982). Some species without dormant buds, however, also achieve high flowering synchrony, although the degree of synchrony was not quantified (Rees 1964).

Second, irrespective of the presence of preformed dormant buds, the type of environmental trigger

affects the probability that other individuals are perceiving the trigger at a comparable time and are beginning or completing flower development and undergoing anthesis at the same time. In the tropics the most unambiguous environmental triggers with the sharpest, most rapid change in environmental conditions appear to be either a rain and change in soil moisture following a drought, or changes in temperature accompanying a tropical storm.

En los trópicos, los factores ambientales más definidos que inician la floración son la lluvia o los cambios de humedad después de una sequía o de temperatura después de una tormenta.

Based on the observation that temperate species known to use photoperiod for diverse developmental phases do not have a high synchrony of those events, photoperiod is less likely to be the cue used by species with such high synchrony of flowering. Photoperiod is known, however, to be involved in tropical species with less synchronous flowering (McClelland 1924, Njoku 1958) and with the initiation of vegetative growth (Stubblebine et al. 1978). Photoperiod may also control the time of floral bud initiation in synchronous species with buds undergoing dormancy and awaiting a second cue for flower anthesis (e.g., coffee, Piringer & Borthwick 1955).

En los trópicos, el fotoperíodo es el factor que influencia las especies con floración menos sincronizada y que puede determinar la iniciación de las yemas florales.

Rain interrupting an extended drought has been implicated as the trigger for many synchronous species in Guanacaste, Costa Rica (Opler et al. 1976, 1980) and on BCI (Augspurger 1982). The brief flowering response for each of these species occurs a consistent number of days after a rain. Repeated waves of synchronous flowering in the liana *Phryganocydia corymbosa* (Bignoniaceae) occur in the wet season in Panama (Gentry 1974). The environmental trigger for this response is undetermined, although it may involve sudden large changes in temperature associated with tropical storms.

Experimental evidence of the environmental triggers for flowering of tropical species with high synchrony is limited. Coffee (*Coffea* sp.) and *Hybanthus prunifolius* both must experience a drought before they will respond to a rapid increase in soil moisture. The environmental change is perceived below ground; sprinkling of the foliage is not necessary to induce flowering in these two species (Alvim 1960,

1973, Augspurger 1982). A leaf water potential of -12 bars is required before the flower buds of *Coffea arabica* can break dormancy. Irrigation brings about the opening of the flowers by a rapid influx of water into the buds in response to the leaf water potential (Magalhaes & Angelucci 1976). In other tropical species with high synchrony of flowering, sharp drops in temperature (Holttum 1949, 1954) and simultaneous changes in temperature and moisture (Kerling 1941) have been experimentally demonstrated or implicated as the trigger.

Hybanthus prunifolius y café requieren de una sequía antes de que respondan a la humedad del suelo y a los cambios percibidos debajo del suelo.

Finally, after the trigger occurs, the amount of development required for flower anthesis influences the variability in timing of the response. Other things being equal, the smaller the flower, the faster the development, and the more advanced the stage of the dormant bud, the less the variation in the onset of flowering. Also, as discussed earlier, the synchrony of the flowering response within the individual influences the intensity of selection for synchrony with others. Generally, greater intra-individual synchrony was found to correlate with greater intra-population synchrony of the onset of flowering (Table 1).

An Experimental Study of Synchrony

An experimental study of *Hybanthus prunifolius* (Violaceae) on BCI (Augspurger 1981) illustrates the interaction between the evolutionary and ecological factors influencing synchrony. The shrub species used in the study occurs in high density on BCI. It forms dormant flower buds in the wet season. It requires a drought before it will respond by flowering 6–7 days after a heavy rain in the dry season (Augspurger 1982). These cue requirements parallel those of coffee (*Coffea* sp., Alvim 1960, 1973). *Hybanthus prunifolius* exhibits an extremely high synchrony of the onset of flowering (Fig. 1).

Different individuals of *Hybanthus prunifolius* were experimentally induced to flower in the forest by sprinkling them with water at different times following a drought during the dry season. A highly asynchronous population was created that was in flower for a 2-month period, although the population naturally is in flower for only 8–10 days. The length of time that any one individual was in flower was not

significantly different between the two groups. Individuals in the induced asynchronous population were compared with those in the highly synchronous population for their ability to attract pollinators and to avoid seed predators.

En la IBC arbustos de *Hybanthus prunifolius* se indujeron a florecer asincrónicamente aplicándoles agua durante la estación seca. Estos individuos trajeron menos polinizadores y sus semillas fueron mayor objeto de predación. Por consiguiente, la sincronización de la floración mejora la adaptabilidad de la población.

Individuals in the induced asynchronous population attracted fewer visits by the pollinator, a social bee. Flowering synchrony in *Hybanthus prunifolius* is followed by a high synchrony of fruit and seed development. The natural synchronous population satisfied the seed predator but individuals in the induced asynchronous population incurred more seed predation. The net effect was that individuals synchronous with conspecifics experienced, on the average, a 10-fold increase over asynchronous individuals in reproductive output, as measured by the number of seeds dispersed. Clearly, the flowering synchrony of an individual with its conspecifics has the potential to greatly influence its overall fitness. Flowering in synchrony with the population had the biggest effect on the reproduction of individuals with the smallest number of flowers. Selection for synchrony therefore also interacts with the size and age of first reproduction.

In this species selection by pollinators and seed predators favors the individual in synchrony with its conspecifics. The individual achieves such synchrony in part by the use of a sharp and unambiguous cue, a heavy rain following a long drought. It is impossible to determine the evolutionary sequence by which these evolutionary and ecological factors affecting synchrony became intertwined. Selection of that particular cue may also relate to other evolutionary pressures, unrelated to synchrony, such as need for water for both flower and fruit. The biotic factors may then be of secondary or reinforcing importance in maintaining the present level of synchrony and the use of that particular cue.

Effects of Subsequent Reproductive Stages

The timing of an individual's later reproductive stages is not necessarily coupled to its timing of

flowering. Selection may act independently on each stage of reproduction. Also, later developmental stages may use other environmental triggers to synchrony from previous stages. Hence high synchrony of flowering is neither a prerequisite for nor a predictor of high synchrony at later stages.

La sincronización de la fructificación no está en correlación con la sincronización de la floración y por eso la selección de la sincronización no es tan intensa.

In general, the longer the time between two reproductive stages—flowering and fruit ripening—the greater the probability that synchrony of the second stage will be lower than the first stage because the intervening stages are more likely to take variable times for different individuals. This prediction assumes that selection for synchrony is not acting independently on the second stage and that no additional trigger to increase synchrony initiates the second stage.

In general, selection for synchrony is likely to be more intense on the flowering stage than on fruit ripening. This is especially true if outcrossing, requiring a high degree of flowering synchrony, is of prime importance: an individual must be synchronous with conspecifics to achieve successful pollen transfer.

Comparable precision of synchrony has not been reported for fruit ripening. Seed dispersal does not require any movement between conspecifics. While attraction of animal dispersers may be enhanced by ripening of fruit synchronously, selection for precise synchrony is not expected. Also species using inanimate agents for dispersal would experience no selection for synchrony of fruit ripening with conspecifics, unless a post-dispersal seed predator is involved. Synchrony of earlier stages in fruit development may also be affected by pre-dispersal seed predators (Janzen 1971).

Synchrony of fruit ripening and seed dispersal is often more difficult to quantify than synchrony of flowering. This is especially true for those species with no clear indicator of when a fruit is fully mature and ready for dispersal. Exceptions to this include species that use inanimate means of dispersal, such as gravitational or explosive devices. In these species, time of dispersal coincides with fruit maturation and thus synchrony is quantifiable. Other examples are species that open the mature fruit for dispersal of arillate seeds. This action clearly demarcates the time of availability of mature seeds.

Synchrony of both flowering and seed dispersal has been quantified for *Hybanthus prunifolius* on BCI.

Seed dispersal in that species is explosive and occurs about one month after flowering; it requires a progressive dehydration of the capsule valves. Its synchrony of dispersal is significantly lower than its highly synchronous flowering (Table 2).

En *Hybanthus prunifolius* la dispersión de semillas ocurre explosivamente un mes después de la floración.

Synchrony of fruit ripening of *Randia armata* (Rubiaceae), an understory tree on BCI, is markedly lower than its highly synchronous flowering (Augspurger, unpublished data). Flowering occurs after a heavy rain in the late dry season or the beginning of the wet season. Over several months the fruits develop slowly to full size; then they remain green and unripe for many months. Finally, up to 18 months after flowering, the fruits ripen to an orange color and are mammal-dispersed. Flowering of the population lasts about 10 days while fruit ripening and seed dispersal occur over a 2-month period.

En *Randia armata* la fructificación no está tan sincronizada como su floración y los frutos son dispersados por los mamíferos.

Seed germination may be synchronous as a carry-over from synchronous flowering and fruiting. However, it is as likely to be asynchronous due to different selection pressures, such as unpredictability of environmental conditions required for seedling establishment. Likewise asynchronous flowering and fruiting may be followed by synchronous germination because of the use of a different environmental trigger for germination.

In *Hybanthus prunifolius* on BCI, seed germination requires a rain trigger; usually the seeds respond to the onset of the wet season. Even with this additional cue, however, synchrony of seed germination is markedly lower than either flowering or fruit ripening in this species. Germination occurs over a 4–5 month period, although 90% is completed within a 6-week period (Augspurger 1979).

La germinación de *Hybanthus prunifolius* responde a la lluvia, pero, aún así, está menos sincronizada que la floración.

Highly synchronous germination may have both positive and negative outcomes. Synchrony may produce density effects by increasing competition among a parent's offspring and with offspring of nearby conspecifics. It may also attract density-dependent herbi-

vores and allow infected seedlings to pass fungal disease to adjacent plants (Burdon & Chilvers 1976, Augspurger, unpublished data). Alternatively, synchrony may produce such a high density of seedlings that the herbivores are satiated (Connell 1971).

Future Directions

The quantification of phenological events of neotropical plants at the population level is in a beginning stage. More such studies are needed, especially in different seasons and in different habitats with different selective forces and environmental triggers of phenological events. Also lacking is a rigorous measure of population overlap incorporating both the entire length of an individual's reproductive phase and variation in number of available reproductive units—flowers/fruits—over that time period. Such a measure would allow a more direct test of the relative potential for outbreeding in different species. A measurement of synchrony of either the onset or the peak day of flowering is insufficient for this use.

La cuantificación de fenómenos fenológicos presenta varias dificultades, sin embargo es necesario esclarecer el valor adaptativo de la variación de diferentes acontecimientos reproductivos.

Particularly lacking are studies comparing the relative synchrony of all reproductive stages of a species and the direction in which synchrony changes during the entire reproductive period. More information is also needed on environmental triggers available, which ones are used by different species, the number of triggers used by a species for its entire reproductive period, and the genetic basis for the timing of reproductive events. Finally, more experimental studies are needed, as they explore the adaptive value of the observed variability in synchrony among different reproductive events and different species.

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