Flowering Patterns in a Seasonal Tropical Lowland Forest in Western Amazonia

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ABSTRACT

The phenological behavior of many tropical plant species is highly dependent on rainfall, but these plants may also respond to changes in photoperiod. Without a better knowledge of the proportion of species responding to different factors, it is difficult to predict how global climate change may affect natural ecosystem processes. The aim of this study was to describe flowering patterns for more than 100 species in Tinigua Park, Colombia, and to propose which factors may trigger flower production (*e.g.*, rainfall, temperature, cloud cover, and photoperiod). Data gathered in 5.6 km of phenological transects during 4 yr and complementary information indicated that the vast majority of species showed intraspecific synchronization, and annual production was the most common pattern, followed by episodic frequency. The annual patterns were common in tree species, while episodic patterns were common in lianas. Simple and multiple regression analyses suggested several aspects of photoperiod as the most likely triggers for flowering in most species. However, the fact that many of these species produce flowers in different periods each year, suggests that the proportion of species responding to photoperiodic cues is less that 23 percent in this community. The flowering times of taxonomically related species seldom showed significantly staggered distributions; however they do not necessarily occur at the same time, suggesting that flowering patterns are not strongly constrained by phylogeny.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: flowering frequency; phenology; photoperiod; plant habits; proximate factors; Tinigua National Park; tropical seasonal forest.

THERE IS GROWING CONCERN REGARDING THE POTENTIAL EFFECTS OF CLIMATE CHANGE on phenological patterns of plants in tropical ecosystems since some studies have documented changes in ecological processes, such as fruit abundance, in association with weather anomalies over the past decades (Chapman *et al.* 2005, Wright & Calderon 2006). Although the evidence suggests that natural ecological patterns may be severely modified by global weather changes, there are two main reasons why it is difficult to generalize and predict changes in the reproductive activity of tropical forest plants in response to climate anomalies. First, weather does not behave the same way in all tropical forests (Malhi & Wright 2004). Second, despite the advances in understanding gross phenological changes at the community level for many tropical ecosystems, we still have a poor knowledge on the proximate causes that trigger phenological processes for the vast majority of tropical plants. Tropical plant communities are composed of a diverse array of species, usually showing a variety of phenological strategies (Rivera *et al.* 2002, Diaz & Granadillo 2005, Singh & Kushawaha 2006), and to date, the effects of proximate factors driving phenological patterns have been assessed with strong experimental evidence for only a few species (*e.g.*, Garwood 1983, Wright & Cornejo 1990, Rivera *et al.* 2002). Furthermore, there is evidence for phenological plasticity for some wide-ranging species (Borchert *et al.* 2004).

Logistic difficulties often impede carrying out experiments to test the effects of variables such as rainfall and temperature changes

that may trigger phenological phases across multiple species (Wright & Cornejo 1990, Graham *et al.* 2003, Diaz & Granadillo 2005). However, strong evidence for some factors may also come from comparative studies lacking experimental manipulations (Rivera *et al.* 2002, Borchert *et al.* 2004), as well as from long-term phenological data bases (Rivera *et al* 2002, Brearley *et al.* 2007), which are not available for many tropical forests (Chapman *et al.* 2005). When climatic information is available, long-term phenological data bases may be the first tools to understand the influence of proximate abiotic variables on the flowering strategies of tropical plant species, and might allow testing models using multisite comparisons.

There is strong evidence that flower anthesis in tropical plants usually occurs during short time windows (Frankie *et al.* 1974, Augspurger 1981, Ashton *et al.* 1988, van Schaik *et al.* 1993, Wright & Calderon 1995, Sakai 2002, Borchert *et al.* 2005, Bendix *et al.* 2006). Intraspecific and interspecific flowering synchronization may occur due to internal physiological processes that are usually triggered by biotic or abiotic proximate factors (Ims 1990, Woolhouse 1992, van Schaik *et al.* 1993, Marques *et al.* 2004). Intraspecific synchronized flowering may have the advantage of permitting cross-pollination and consequent high levels of gene flow (Faegri & van der Pijl 1979, Augspurger 1983, Tutín & Fernandez 1993, Sakai 2002). Interspecific synchronization may result in fitness advantages when predator satiation and shared attraction of pollinators occurs (Janzen 1971, Augspurger 1981, Ashton *et al.* 1988, van Shaik *et al.* 1993), but it may also produce negative effects such as hybridization and interspecific competition for pollination (Kenrick 2003, Pellegrino *et al.* 2005).

Traditionally, biotic processes have been hypothesized as the ultimate causes influencing the evolution of the phenological patterns, whereas abiotic factors have been invoked as proximate causes of flowering. Among biotic processes, herbivory and seed predation avoidance have been argued to be the main advantage of phenological synchronization in a variety of tropical environments, including the masting patterns typical of many forests in SE Asia (Janzen 1971, Augspurger 1981, Ashton *et al.* 1988, Curran & Webb 2000, Curran & Leighton 2000, but see Sakai 2002). Pollination has also been suggested to play an important role in the evolution of flowering patterns, since many agents may present seasonal activity patterns, such as bees, which are important pollinators in tropical forests (Gentry 1974a,b; Sigrist & Sazima 2004; Ramirez 2006). The timing of seed dispersal, germination, and young seedling development seems to be the major factor responsible for synchronized production of fleshy fruits at the beginning of the rainy season in many tropical forests (Garwood 1983, van Schaik *et al.* 1993). This pattern has been interpreted as an advantage for young seedlings in order to survive early establishment during a period when drought is unlikely (Garwood 1983).

Several studies have shown that rainfall patterns are responsible for the seasonal cycles of growth, leaf abscission, and flowering for some species in tropical environments (*e.g.*, Medway 1972, Croat 1975, Reich & Borchert 1982, Sahagun-Godinez 1996, Borchert 1998, Borchert *et al.* 2004, McLaren & McDonald 2005, Sakai *et al.* 2006, Brearley *et al.* 2007). In many seasonal forests, most canopy plants flower during droughts (van Schaik *et al.* 1993), and several hypotheses have been proposed to explain this pattern (*i.e.*, water stress inhibition, physical obstruction for pollination, exposure to pollinators, and more pollinator abundance; Janzen 1967). Perhaps the most important influence of rainfall is its role on the physiological processes promoting bud breaking and subsequent flowering (Augspurger 1981).

Temperature is another variable capable of triggering flowering and affecting plant metabolism (Lyndon 1992). Changes in temperature are correlated with flowering events and other phenological cycles in many tropical environments (Ashton *et al.* 1988, Morellato *et al* 2000, Marques *et al.* 2004, Corlett & Lafrankie Jr. 1998, Tutín & Fernandez 1993, Stevenson 2004). However, in very few cases has it been demonstrated that the patterns are triggered by temperature and not by covariates. For example, changes in solar radiation may also affect phenological patterns and they tend to be associated with changes in temperature. There is strong evidence showing how cloud cover and radiation affect fruit and flower production, as well as plant development (Wright & van Schaik 1994, Wright *et al.* 1999, Bettina *et al.* 2002, Graham *et al.* 2003, Stevenson 2004, Hamann 2004, Yeang 2007, Zimmerman *et al.* 2007).

Similarly, changes in photoperiod have been associated with flowering patterns (Marques *et al.* 2004, Stevenson 2004, Borchert *et al.* 2005, Sloan *et al.* 2007). However, the photoperiod is independent of climate and does not show interannual variation. Many of the species experimentally tested have shown flowering responses associated to photoperiod (Lyndon 1992). Even in tropical latitudes, where differences in day length are not as evident as in temperate regions, photoperiod variables may induce flowering (Borchert

& Rivera 2001, Borchert *et al.* 2005). It is relatively easy to test photoperiod as a trigger of phenological phases, since the responses are expected to occur within a short window of time at the same moment every year at each site (Rivera & Borchert 2001).

Several studies have found differences in flowering phenology among habit types (Croat 1975, Morellato & Leitao-Filho 1996, Sahagun-Godinez 1996, Ramírez 2002). For instance, in Barro Colorado Island, Croat (1975) found that habit types directly exposed to sunshine such as canopy trees, lianas, and epiphytes show discrete seasonal flowering in dry periods, whereas terrestrial herbs and shrubs produce flowers during extended periods in the rainy season. These differences seem to be caused by the differences in radical systems, particular nutrient requirements, and capabilities of nutrient storage (Marques *et al.* 2004).

There is also evidence of similar flowering patterns among taxonomically related species. Some studies have suggested phylogenetic constraints to be the cause for these patterns (Johnson 1992, Lyndon 1992, Wright & Calderon 1995, Bawa *et al.* 2003). However, such patterns are also expected under adaptive hypotheses, like for instance when there are advantages for all species to flower at a particular time. Related plant species usually have similar morphology and might share pollinators (Gentry 1974a, Temeles *et al.* 2000, Temeles & Kress 2003); therefore the synchronization of flowering periods may originate competition for pollinators among sympatric species. If competition for pollinators is strong, selection should favor staggered patterns of flowering production, with little overlap. Although these patterns have been described in some guilds (Gentry 1974a, Stiles 1975, Williams *et al.* 2001), the interpretation in relation to competition has been controversial (Levin & Anderson 1970).

Given the scarcity of data bases and our limited understanding of phenological processes in tropical lowland forests, the main goal of this study was to describe the flowering patterns for the main species comprising the plant community at Tinigua National Park, northwestern Amazonia, Colombia. Particularly, we asked the following questions: (1) Is there intraspecific flowering synchronization? (2) What is the pattern of flowering frequency for each species? (3) Is there a relationship between flowering frequency and habit type? (4) Which are the abiotic variables with highest potential for triggering flowering events? (5) Is the flowering time of taxonomically related species staggered (as expected from pollinator competition) or clumped (as expected from phylogenetic inertia)?

METHODS

STUDY SITE.—This study took place in a tropical rain forest on the eastern border of Tinigua National Park, west of La Macarena mountains, Meta, Colombia (Stevenson *et al.* 1994). The study site consisted of three research stations along a 5 km stretch of forest along the west bank of the River Duda (2°40′ N, 74°10′ W, 350–400 m asl; Stevenson 2002). Rainfall is seasonal in the region, with a dry period occurring between December and March (Fig. 1A). Average annual rainfall and temperature estimates at the
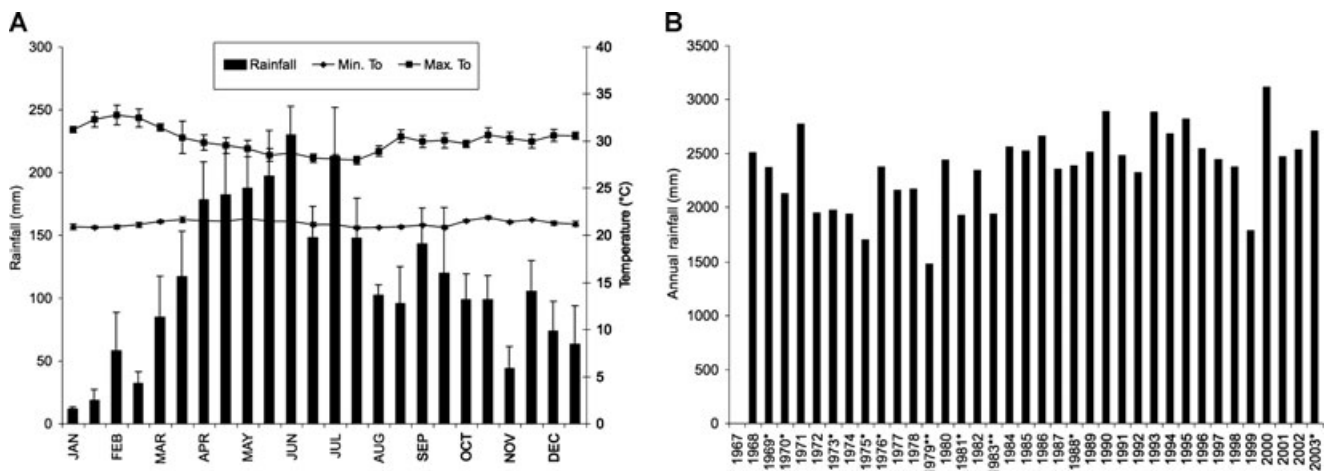
FIGURE 1. Main climatic variables in the study region. (A) Mean monthly precipitation, maximal and minimal temperatures in Tinigua Park during the study periods. (B) Annual rainfall in the nearest town (La Macarena) at about 75 km from the study site. The number of asterisks indicate incomplete information (* = 1 mo, ** ≥ 1 mo).

research station between 1989 and 1993 were 2622 mm and 25°C, respectively (Kimura *et al.* 1994). Rainfall patterns have shown low variability in the region across years (Fig. 1B).

FIELD PROTOCOL AND DATA ANALYSES.—We gathered phenological data during four yearly cycles, two of which were consecutive (March 1990–April 1991, August 1996–July 1997, February 2000–January 2001, and February 2001–January 2002). Community-wide information was recorded in 12 phenological transects (*ca* 450 m, total length = 5.6 km), which were monitored biweekly (Stevenson *et al.* 1998). We recorded all individuals with open flowers for all species of trees dbh > 5 cm and lianas dbh > 2 cm detected on transects. For smaller trees and lianas, as well as for herbs, the frequency of transects where they were detected was noted, but individuals were not counted separately. Each recording of an individual with flowers (or a transect in the case of small plants) was considered a 'flowering event' for a plant species and a statistical unit for the analyses. If the same individual was registered as in bloom in consecutive biweekly checks, each recording was considered a separate event.

For the first study period only, flowering was inferred from data on ripe fruits and estimates of the time necessary to develop ripe fruits based on the other 3 yr, when we noted both flowering and fruiting events (Cortes 2005). These estimates were used only for species showing low variation in maturation time (variance in developing time less than three biweekly periods).

To estimate intraspecific synchronization we included only species with at least five flowering events in at least 1 yr. Vector algebra was used to quantify the degree of synchronization for 122 plant species. The 2-week periods were converted to angles, from 0° (= first biweekly period of January) to 345° (= last biweekly period of December), at intervals of 15°. We calculated the vector length (*r*) following the method used by Wright and Calderon (1995):

$$r = (x^2 - y^2)/\Sigma n_i$$

where $x = \Sigma n_i \cos \theta_i$, $y = \Sigma n_i \sin \theta_i$, and n_i is the number of flowering events in biweekly period i. To obtain a valid number for the angle, if $x > 0$ then $\theta = \arctan (y/x)$ and if $x < 0$ then $\theta = 180 + \arctan (y/x)$. Thus, vector length r ranges between zero (when an equal number of flowering events occur each month, indicating lack of synchrony) and one (when all events occur in 1 mo, indicating synchronization). To calculate the probability of finding a particular vector length by chance, we constructed a distribution of vector lengths from 2000 simulations, where the monthly order of flowering events was chosen at random. The distributions from the simulations were compared with the actual r value in order to verify the significance at $P < 0.05$, which varies depending on the number of flowering events noted each year (Fig. 2A). This statistical procedure leads to similar results if we follow the Rayleigh test (Zar 1999; results not shown).

The frequency of flower production of each species was classified as continuous, episodic, annual, or supra-annual (Newstrom *et al.* 1994, Bawa *et al.* 2003). Continuous species show flowering events along the year for > 6 mo. Episodic species produce flowers more than once a year in discontinuous events that in total sum up to < 6 mo. Annual species produce flowers once a year and supra-annual species do not produce flowers every year. Species showing variations across years were classified in the most frequent category (*e.g.*, a species showing episodic flowering 1 yr and annual flowering in 2 yr was classified as annual). In some potentially ambiguous cases additional observations from botanical vouchers and studies on primate diets were used as well (Stevenson *et al.* 2000a,b; Stevenson 2006). We used contingency tables to assess the association between growing habits and flowering frequency. All species detected with flowers on transects were classified in one of five growing habits: trees (including palms), bushes and small trees (< 8 m height), herbs, lianas, and epiphytes. Supra-annual species were excluded because their low frequency did not suit to the requirements of G tests (Sokal & Rohlf 1995).
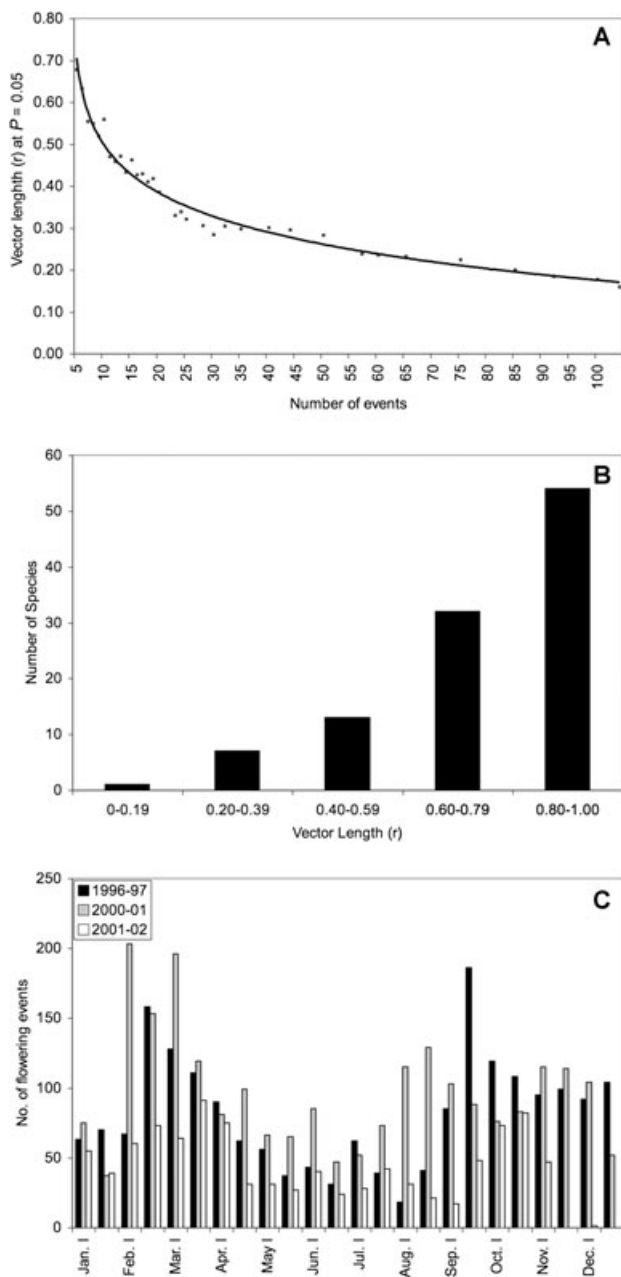
FIGURE 2. Null model to assess intraspecific synchronization and patterns of interspecific synchronization. (A) Significance of vector length (r) as a function of the number of flowering events per species. (B) Frequency distribution of vector lengths for all plant species included in the study at Tinigua Park. (C) Frequency of flowering events during the main study years.

We used linear and multiple regression analyses to explore potential association between the number of flowering events for each species and a number of independent abiotic variables related to rainfall, temperature, cloud cover, and photoperiod. During the study we measured daily rainfall, minimal and maximal temperatures, and cloud cover, quantified as an index 0–

5 (0 = sky completely clouded over and 5 = no clouds). Photoperiod variables included the period of equinoxes, day length, sunset, and sunrise times. We also included the monthly magnitude of change in the last three parameters and their period of maximum change. All photoperiod variables were extracted from http://www.geocities.com.jjlammi/. We excluded some abiotic variables that were highly correlated ($r_s > 0.80$) with other independent variables (*e.g.*, number of dry days, number of rainy days, mean temperature, mean maximal temperature, sunset time, and acceleration in sunset time). Thus, we finally included four variables associated with rainfall patterns (biweekly rainfall, precipitation after a dry period, time of the first heavy rain after the main dry season, and number of continuous dry days), five with temperature (mean lowest daily temperature, lowest temperature in the biweekly period, highest maximal temperature, mean difference between daily maximal and minimal temperatures), one with cloud cover (our index of cloud cover), and six with photoperiod (day length, equinox occurrence, change in day length, maximal day length acceleration, sunrise time, and maximal acceleration in sunrise time). To assess the effect of each of these variables, we first used simple regressions between the number of flowering events for each species ($N = 132$) and each abiotic variable. Because the effect of a variable might not be immediate but be delayed in time, we also regressed time lags of flowering events up to 4 mo with each abiotic factor. Then we fitted a stepwise regression model to the data, including variables with significant associations ($P < 0.05$), using JMP (SAS Institute 1994). When a single variable showed significant coefficients of determination for more than one lag, only the lag with the highest coefficient was included in the stepwise analysis. This should be considered an exploratory approach to look for associations and not strictly hypothesis testing. Since the number of flowering events was low for many species and the number of independent variables (including lags) was high, some statistically significant associations could require further investigation.

In addition, we checked the potential role of photoperiod as a factor triggering flowering, based on the consistency in the flowering period in different years. That is, we discarded as photoperiod-induced plants, all species showing flowering events in > 2 mo in all study years. For instance, a species flowering in January and February all years was categorized as potentially induced by photoperiod, but a species flowering in January one year and in March any other year was categorized as not induced by photoperiod.

FLOWERING PATTERNS OF RELATED SPECIES.—To determine whether flowering patterns of taxonomically related species overlap in time to a greater or lesser extent than expected by chance, we used a null model based on correlation coefficients. We included 14 families well represented in the data set (Annonaceae, Apocynaceae, Arecaceae, Bignoniaceae, Burseraceae, Euphorbiaceae, Fabaceae, Heliconiaceae, Lecythidaceae, Malvaceae, Meliaceae, Mimosaceae, Moraceae, and Rubiaceae). For each pair of species within families, we first calculated the correlation coefficient between the number of flowering events occurring on each one of all biweekly periods. High coefficients would indicate similarity in the timing of flower anthesis between the species pairs, low coefficients no associations, and

negative correlations nonoverlapping distributions. The significance of the correlation coefficients was inferred from null distributions, where 1000 coefficients were calculated for each pair after altering the order of flowering events at random for each biweekly revision within each year. We used only the data from the last 3 yr of study for these analyses.

RESULTS

INTRASPECIFIC SYNCHRONIZATION.—The distribution of mean vector lengths for 122 species analyzed was biased toward high values (Fig. 2B), implying that the majority of these species showed flowering synchronization. Only 28 species (23%) showed years in which flowering events were not statistically different from events randomly distributed in time. Furthermore, some of these species showed synchronization in some years and only 7 percent of the species consistently showed lack of synchronization. Similarly, the percentage of yearly records when a species was found to be unsynchronized was low (12.4%, $N = 306$). There was a tendency toward a higher proportion of synchronized species in the canopy (trees and lianas: 80%) than in the understory (shrubs, treelets, and herbs: 68%); however, this trend was not significant ($G = 2.2$, $P = 0.14$).

FLOWERING FREQUENCY.—It was possible to assess the flowering frequency of 196 species from the plants on transects and additional information (Appendix S1). The majority of these species showed annual patterns of flower production (56.6%), followed by episodic (29.6%), continuous (12.8%), and supra-annual (1.0%) patterns. Flowering patterns were strongly associated with growth forms ($G = 40.3$, df $= 8$, $P < 0.001$). The most evident differences were for the large proportion of trees with annual flowering patterns, and the high frequency of lianas with episodic flowering events (Table 1).

POTENTIAL FLOWERING TRIGGERS.—A total of 132 species were analyzed for flowering triggers and all showed significant coefficients of determination in simple regression analyses trying to predict the number of flowering events from abiotic factors. The single

variable with the highest coefficient of determination was 0.61, and for most species, the maximum coefficient only explained 10–20 percent of the variation in flowering events (Fig. 3A). The maximum coefficients of determination tended to be higher for variables related to photoperiod than for rainfall, temperature, and cloud cover (Fig. 3B.). In only a few multiple regression analyses, the overall model explained > 60 percent of the variation in the number of flowering events (Fig. 3A.). For 40 species for which the multiple coefficient was higher than 0.6, the most important factors remaining highly significant ($P < 0.01$) were related to photoperiod and rainfall (Appendix S2). Flowering in nine of these species was associated with photoperiodic factors, in six with rainfall, and in two with temperature. Flowering in other species seemed to be associated with more than one factor (10 species with photoperiod and rainfall variables, four with photoperiod and temperature, three with rainfall and temperature, and six with photoperiod, rainfall, and temperature).

Overall, variables related to photoperiod were included in the models for a large proportion of the species with highly predictive models (73%). However, in the second analysis, including a larger number of species ($N = 169$), when the species were assigned to the category of potentially induced by photoperiod (*i.e.*, showing flower production in a narrow window of time in all years), this was just 23 percent of species .

FLOWERING PATTERNS OF TAXONOMICALLY RELATED SPECIES.—We calculated 286 correlation coefficients between flowering events of pairs of species belonging to the same family. Most (200) showed values indistinguishably different from random temporal patterns. The remaining paired comparisons showed almost twice the number of positive (56) than negative coefficients (30). For nine families we found more positive than negative coefficients, two plant families showed similar number of positive and negative coefficients, and only three families showed a preponderance of negative coefficients (Table 2).

DISCUSSION

FLOWERING FREQUENCY AND SYNCHRONIZATION.—Most plant species at Tinigua showed synchronized patterns of flower anthesis, with annual and episodic frequencies. These results are common in tropical forest, where the majority of the species are pollinated and dispersed by animal vectors (Kelly & Sork 2002).We found strong associations between growth forms and flowering frequency, supporting the results found in previous studies (Croat 1975, Sahagun-Godinez 1996, Morellato & Leitao-Filho 1996, Ramírez 2002, Marques *et al.* 2004). Very few species showed supra-annual patterns of production, in sharp contrast to the masting strategies of many tropical forests in Southeast Asia and in temperate regions (Herrera *et al.* 1989, Sakai 2002). It may be argued that, because our study included nonconsecutive years, some supra-annual species might have been overlooked, producing an underestimate of the frequency of this type of plants. However, the proportion of tree species registered in 7-ha vegetation plots (Stevenson 2002), which

TABLE 1. *Association between plant growth forms and flowering frequency in Tinigua National Park. Two tree species with supra-annual patterns were excluded from the analysis.*

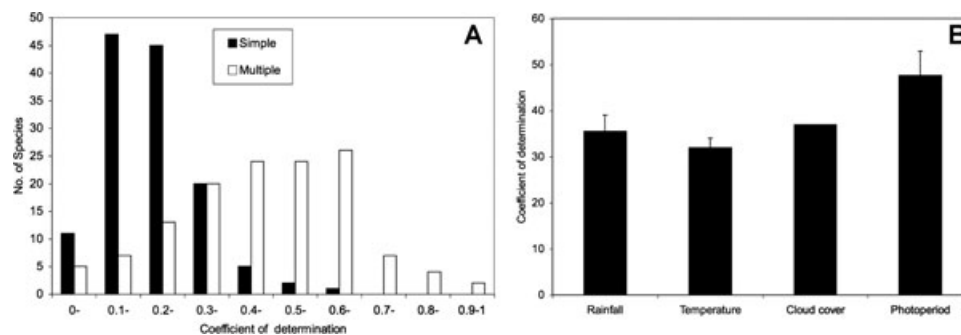| Habit	Annual	Continuous	Episodic	Total
Trees/palms	71	10	19	100
Shrubs/treelets	10	2	8	20
Lianas	16	1	24	41
Herbs	7	4	5	16
Epiphytes	7	8	2	17
Total	111	25	58	194

FIGURE 3. Comparison of the relative importance of proximate factors associated with flowering in Tinigua National Park. (A) Frequency distribution of coefficients of determination for the plant species studied. Black bars represent simple regression analyses and white bars represent multiple stepwise regression analyses. (B) Mean of the maximum coefficients of determination for each of the main abiotic factors explaining the number of flowering events for 132 species studied. SEs are shown above the bars.

TABLE 2. *Number of paired comparisons in flowering time between species belonging to the same plant family (based on correlation coefficients). The probability of finding a coefficient significantly different from random expectations was calculated from a distribution of 1000 coefficients estimated from rearranging the number of events between each pair of species at random times. The analyses included 87 plant species from well-represented families in the flora of Tinigua National Park, Colombia.*

Family	Positive coefficients	Negative coefficients	Neutral coefficients	No. of spp.	No. of comparisons	Family mean
Annonaceae	2	1	3	4	6	0.08
Apocynaceae	4	0	6	5	10	0.13
Arecaceae	8	0	13	7	21	0.16
Bignoniaceae	18	4	69	14	91	0.09
Burseraceae	3	1	2	4	6	0.16
Euphorbiaceae	0	1	2	3	3	−0.03
Fabaceae	3	3	30	9	36	0.01
Heliconiaceae	1	0	2	3	3	0.12
Lecythidaceae	2	1	3	4	6	0.10
Malvaceae	7	10	19	9	36	0.03
Meliaceae	1	1	13	6	15	0.03
Mimosaceae	1	6	8	6	15	0.02
Moraceae	3	2	23	8	28	0.05
Rubiaceae	3	0	7	5	10	0.20
Total	56	30	200	87	286	0.07

were also noted in phenological transects was high (80%), suggesting that the proportion of missing supra-annual species could not be higher than 20 percent. Furthermore, 78 percent of the missing species had very low densities (< 0.1 ind/ha), suggesting that they were not registered because of their low abundance and not for being supra-annual. We think we missed some species that may show supra-annual patterns of production (*e.g., Guadua angustifolia*), but from this approach and additional observations during other years, we are confident that the proportion of this supra-annual plants in the study area is low.

In spite of the bimodal pattern of flowering episodes along the year at the community level (Fig. 2C), there is only one peak of fruiting in this community, which takes place at the beginning of the rainy period (Stevenson 2004). Many Neotropical forests show fruiting peaks at the beginning of the rainy period (Frankie *et al.* 1974, van Schaik *et al.* 1993, Morelatto & Leitao-Filho 1996, Stevenson *et al.* 1998, Haugaasen & Peres 2005, Wright & Calderon 2006), suggesting that different plant species flowering prior to this time have adjusted development time to ripen fruits as the rains begin. These patterns support the hypothesis advocating advantages in fruit ripening and seed dispersal at the beginning of the rainy period (which occurs once a year in places with unimodal rainfall, as in our study site), when germination may be induced and the seedlings would start growing in a season with low probability of droughts (Garwood 1983). Fruiting peaks at the community level may also be favored by selection to avoid seed predators through satiation effects due to temporal and spatial aggregation of seeds (van Schaik *et al.* 1993).

Episodic flowering was the second most common strategy, and was common in vines (*e.g.*, Bignoniaceae), which do not invest much energy in supporting structures and might allocate more resources to reproduction than trees. Some tree species showed variation in flowering frequencies (*e.g.*, *Brosimum alicastrum* and *Pseudolmedia* spp.) and presented episodic flowering only in some years. It is possible that good years in terms of irradiance may allow these species to reproduce several times a year. Interestingly, most of these episodes occurred in the dry season in 2000 after a year with low regional mean annual precipitation (Fig. 1B), suggesting high irradiance in the previous year. Furthermore, fruit production and the frequency of flowering events was low in 2001 (Fig. 2C). Therefore, climate anomalies may influence phenological behavior in this community in a similar way found in tropical forests affected by El Niño events (Wright *et al.* 1999). Plasticity allowing episodic flowering and frequent reproduction may be one of the causes for the increase in adult and regenerating vines on fragmented and continuous Amazonian forests, which have been exposed to high radiation in the last decades (Phillips *et al.* 2002, Benitez & Ramos 2003).

Continuous flowering was relatively rare and was common only among three main plant groups: figs, some palms, and some terrestrial herbs. It is well established that the reproductive strategy of figs depends on continuous reproduction to support the populations of their obligate pollinator wasps (Kjellberg *et al.* 1987). For palms and herbs, it is not clear why some species show continuous flowering, and there are many species with different patterns. Terrestrial herbs on the forest floor may be very limited by radiation and it is possible that their timing for reproduction may depend more on gathering enough energy for reproduction than on environmental clues (Wright & van Schaik 1994).

POTENTIAL FLOWERING TRIGGERS.—No single abiotic variable was able to predict a large proportion of the variation in the number of flowering events for any species. The results from both the simple and the multiple regression analyses suggested that variables related to photoperiod may be the most likely triggers for the species studied (54% and 73% species, respectively). However, these models are based on statistical associations that do not prove causation. In fact, the second analysis showed that only 23 percent of the species in Tinigua may bloom in response to photoperiod because they may produce flowers at different periods each year. Similarly, for some of the species included in this study, experimental studies have provided strong support for other environmental triggers. In the specific case of *Hybanthus prunifolius*, flowering occurs after the first heavy rains and it may be induced by experimental watering (Augspurger 1981). Our stepwise regression model for *H. prunifolius* revealed a strong association not only between the number of plants flowering and the occurrence of the first rains (two weeks lag: $F = 20.9$, $P < 0.0001$), but also with the number of continuous dry days ($F = 6.44$, $P = 0.01$) and two variables related to temperature (*e.g.*, difference in temperature in 2-mo lag: $F = 34.9$, $P < 0.0001$). If we assume the strong experimental evidence as true, then we are either suggesting three spurious associations with noncausal variables or documenting geographical variation in the flowering strategy of this species. Therefore the models generated here should be considered as hypotheses to be tested (Appendix S2). It would be possible to check the importance of many of the potential factors suggested in this study as triggers for each plant species by experimental and comparative studies using other data bases and herbarium labels.

There are two main reasons for finding low coefficients of determination in the analyses of potential triggers. First, it is possible that we were not considering or evaluating the true factors. For instance, it was suggested that some species in Africa flower after a period of some days with temperatures < 19°C (Tutin & Fernandez 1993). We did not use specific temperature values as variables in our analyses because changes in minimal temperature are quite small in our study place. However, we cannot be sure if other factors associated with rainfall, temperature, radiation, or photoperiod will provide better models. In addition, it is possible that biotic factors such as pheromones are the most important cues, but these variables remain unstudied. New findings on internal plant physiology and chemical communication among plants may offer some of the elusive answers in the phenology of tropical plants (Ims 1990). Second, it is possible that the variables triggering flowering were indeed quantified and included, but there are developmental delays until the process of anthesis, which could obscure the associations. This is unlikely, since the highly intraspecific synchronized patterns found in the study would not be expected under large developmental variation.

FLOWERING PATTERNS OF TAXONOMICALY RELATED SPECIES.—The analysis of taxonomically related species showed a large number of paired comparisons with correlation coefficients similar to those expected from random flowering events in time. This result suggests there are weak to inexistent directional selection pressures to disaggregate the flowering times of species with potential competition for pollinator agents, as it has been demonstrated in other floras (Boulter *et al.* 2006), or alternatively that plants cannot respond to selection if it does exist. In addition, the fact that positive correlation coefficients were much more common than negative coefficients, indicates that phylogenetic inertia or shared adaptive responses are much more common than pressures to avoid competition for pollinator agents.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Appendix S1. *Plant species included in the study, showing their habit, flowering months and the number of individuals on transects, and the frequency of production.*

Appendix S2. *Species showing high predictive power in multiple regression models explaining the variation in flowering episodes from abiotic variables in Tinigua Park.*

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