

Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance

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Abstract: The seasonality of both rainfall and solar irradiance might influence the evolution of flowering and fruiting in tropical forests. In seasonally dry forests, to the degree that soil moisture limits plant productivity, community-wide peaks in reproduction are expected during the rainy season, with seedfall and germination timed to allow seedlings to become well established while soil moisture is available. Where soil moisture is never seasonally limiting, seasonal changes in light availability caused by periods of cloudiness or seasonally low zenithal sun angles should favour reproduction during seasons when irradiance levels are high. To evaluate these predictions, we documented the timing of flower and fruit fall for 10 and 15 y at El Verde, Puerto Rico, and Barro Colorado Island (BCI), Panama. At El Verde, rainfall is abundant year-round and solar declination largely determines seasonal variation in irradiance. At BCI, rainfall is abundant throughout the 8-mo wet season while drought develops and average solar irradiance increases by 40–50% over the 4-mo dry season. Seasonal variation in the number of species flowering and fruiting at both sites was generally consistent with the hypothesis that seasonal variation in irradiance limits the evolution of reproductive phenologies. Community-level metrics provided no evidence for a similar role for moisture availability at BCI. Seasonal variation in irradiance also strongly influenced seed development times at both sites. Thus, community-wide phenologies reveal a strong signature of seasonal changes in irradiance, even in those forests that exhibit some degree of seasonality in rainfall.

Key Words: Barro Colorado Island, Panama, Luquillo Forest Dynamics Plot, phenology, Puerto Rico, rainfall, reproduction, seasonality, solar irradiance

INTRODUCTION

Seasonal variation in the availability of water and light should place physiological and thus evolutionary constraints on the phenologies of tropical forest plants (van Schaik *et al.* 1993, Wright 1996). Available water is required to ensure the positive turgor pressures necessary to expand growing cells during leaf flush, flowering and fruit development. Therefore, seasonal drought is expected to be a key selective factor in the reproductive phenologies of many plant species in seasonally dry tropical forests (Augspurger 1983, Borchert 1994, Bullock 1995, Foster 1982, Frankie *et al.* 1974, Lieberman 1982, Lieberman & Lieberman 1984, Newstrom *et al.* 1994, Opler *et al.* 1976, 1980;

Rathke & Lacey 1985, Shukla & Ramakrishnan 1982, Wright 1991). When water is available, however, light is likely to limit photosynthetic carbon uptake and primary production because leaf area indices are high (up to five or six units of leaf area for each unit of ground area) and most leaves are deeply shaded (Graham *et al.* 2003). Van Schaik *et al.* (1993) and Wright & van Schaik (1994) hypothesized that plants which produce new leaves and flowers when light levels are maximal accrue two selective advantages: (1) since photosynthetic assimilation rates are greatest in new leaves, photosynthesis is maximized by producing new leaves during the sunny season and (2) assimilates are more efficiently transferred directly to growing organs during the sunny season rather than translocating and storing them in different tissues only to mobilize and translocate them at a later time to the developing flowers and fruits. Graham *et al.* (2003) recently showed experimentally that wet-season cloud

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cover limits annual assimilation for an upper canopy tree species, confirming earlier circumstantial evidence that tropical trees are light-limited during cloudy periods. Thus, all else being equal, tropical trees should be under selection to flush new leaves and reproduce during periods of high irradiance.

In seasonal tropical forests, the seasonality of rainfall and incoming solar irradiance are often very different and both might influence the evolution of plant phenologies (Hamann 2004, van Schaik *et al.* 1993). The timing of potential water limitation and potential light limitation differ because the water vapour in clouds and humid air absorbs a substantial portion of photosynthetically active radiation (PAR). Thus, compared to the annual average, seasonal forests often receive 25–50% more PAR during the dry, sunny season when water is potentially limiting and 20–33% less PAR during the cloudy, rainy season when water is not limiting (Wright & van Schaik 1994). Access to soil water either through rooting in moist microsites or through deep roots that reach moist soil horizons might allow particular species to produce flowers and fruits during the sunny dry season in seasonally dry forests (Borchert 1994, Wright 1996). A final possibility, stem storage of water, might sustain transpiration for part of one day (James *et al.* 2003, Meinzer *et al.* 2004) and is unlikely to sustain the positive turgor potentials required to expand reproductive organs.

The seasonal movements of the Intertropical Convergence Zone (ITCZ) cause the alternation of wet and dry seasons near the equator. The ITCZ forms where the zenithal sun most heats the atmosphere, but its position lags behind the zenithal sun by 1–2 mo due to atmospheric inertia. The tradewinds bring moisture-laden air into the ITCZ, where the warmed air rises creating a band of heavy cloud cover and precipitation around the globe (McGregor & Nieuwolt 1998). Because the movement of the ITCZ results in a close temporal conjunction of maximum seasonal irradiance and the onset of seasonal rains, inferences concerning the ultimate selective cause of dry-season flowering and fruiting in seasonal tropical forests have been problematic (van Schaik *et al.* 1993). In particular, it is unclear whether the peak in community-wide flowering in the dry season reflects selection to time reproduction with peak seasonal irradiance or to ensure seed dispersal at the onset of seasonal rains or both (Garwood 1983, Wright & van Schaik 1994).

The impact of the ITCZ in the Caribbean Sea is limited to approximately 16°N (McGregor & Nieuwolt 1998). Thus, islands between 16° and 23.5°N are more strongly impacted by the north-east trade winds. Rainfall is related to storms coming from the West Atlantic during June to December (which sometimes develop into hurricanes) and storm fronts pushing down from the north from January to May. In montane forests, these seasonal patterns

combine with orogenic storms originating from moisture in the prevailing trade winds to cause high rainfall at all times of the year. Because cloudiness is relatively constant throughout the year, changes in solar irradiance are largely determined by seasonal changes in maximum zenithal sun angle. This provides an opportunity to evaluate the hypothesis that the evolution of reproductive phenologies is determined by seasonal variation in light levels without the confounding influence of seasonal drought. Thus, in ever-wet forests, where rainfall always exceeds potential evapotranspiration, limitation by moisture availability does not occur (except during rare, unpredictable droughts; Beard *et al.* 2005) and the timing of flower and fruit production is predicted to track the seasonality of incoming solar irradiance.

We tested the dual roles of moisture and light limitation in determining the phenologies of tropical forests by contrasting one ever-wet site and one seasonally dry site. We compare the Luquillo Forest Dynamics Plot in El Verde, Puerto Rico (18°N; 400 m asl), where monthly rainfall averages more than 200 mm throughout the year, and the Barro Colorado Island (BCI) Forest Dynamics Plot in Panama (9°N; 170 m asl), where there is a 4-mo dry season, to address four hypotheses.

Hypothesis 1: Reproductive activity is greatest during sunny seasons and lower during seasons of low irradiance. At El Verde, seasonal light levels are primarily driven by changes in solar declination. Thus, if the timing of reproduction has responded evolutionarily to seasonal variation in light levels, the number of species flowering and fruiting should be greatest around the summer solstice when light levels are highest and least around the winter solstice when light levels are lowest. In contrast, peak solar irradiance occurs during the dry season on BCI when cloud cover is least in February, March and April. Thus, if reproductive timing has evolved in response to seasonal variation in light levels on BCI, the number of species flowering and fruiting should be greatest in February, March and April and least during the late wet season toward the end of the 8-mo wet season and near the winter solstice.

Hypothesis 2: Reproductive activity is greatest during the rainy season and lower during the dry season when moisture availability limits plant function. If drought limits the evolution of flowering and fruiting times on BCI, the number of species reproducing should decline throughout the late dry season as drought develops and be greatest throughout the wet season. Hypotheses 1 and 2 lead to incompatible predictions for BCI.

Hypothesis 3: Seed development times should be shortest during sunny periods. Seasonal differences in irradiance might also affect the evolution of fruit development times, which are predicted to be shortest during periods of high irradiance and longest during periods of low irradiance.

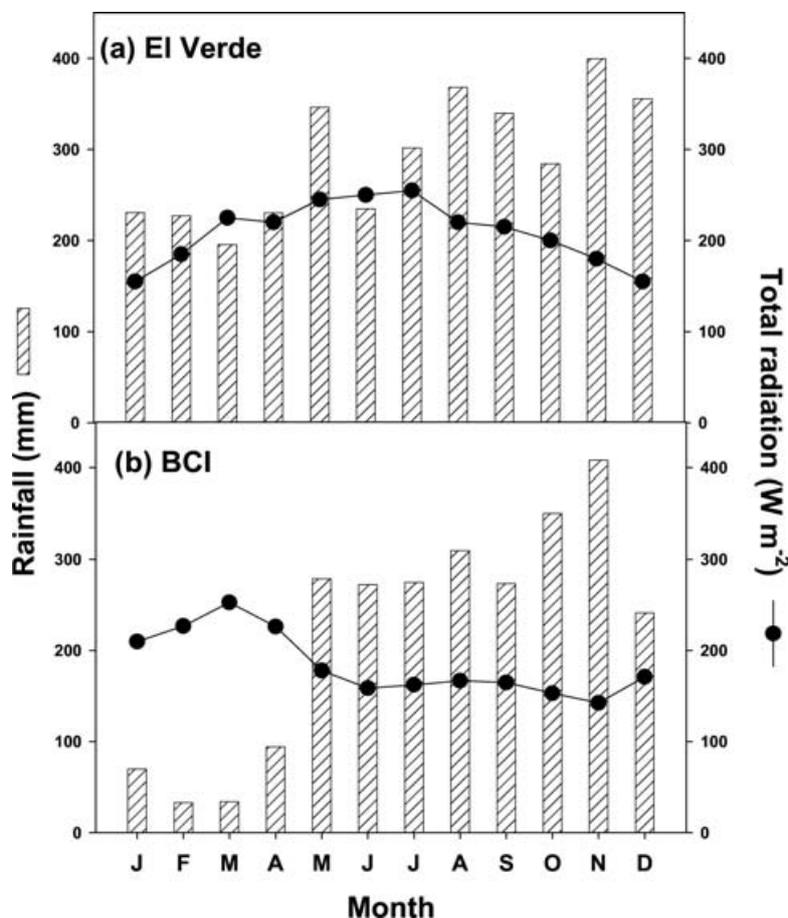


Figure 1. Rainfall and solar irradiance at El Verde (a) and Barro Colorado Island (b). Rainfall data were collected at El Verde Field Station (1975–2002) and total solar irradiance data were collected at the Bisley Experimental Watersheds (1998–2000) in the Luquillo Experimental Forest, Puerto Rico. Rainfall (1929–2002) and total solar irradiance (1984–2002) for BCI.

Hypothesis 4: Phenologies of eight species held in common at El Verde and BCI will either converge on the local community-wide pattern or reflect an ecological filter. If reproductive phenologies are evolutionarily plastic and Hypothesis 1 proves to be correct, shared species should concentrate flowering and fruiting near the summer solstice at El Verde and in the dry season at BCI. Alternatively, if reproductive phenologies are evolutionarily fixed and conditions that favour reproduction establish an ecological filter on the distributions of species, shared species should be drawn from those that reproduce in the wet season on BCI and should have similar reproductive phenologies at the two sites.

METHODS

Study sites

The Luquillo Forest Dynamics Plot (LFDP; Thompson *et al.* 2002, Zimmerman *et al.* 1994) is located near the El Verde

Field Station in eastern Puerto Rico at 18°19'N, 65°49'W. Annual rainfall averages 3500 mm and no month averages less than 200 mm (Figure 1a). The El Verde climate is technically 'aseasonal' or ever-wet because no month receives < 100 mm of rain (McGregor & Nieuwolt 1998), even though some seasonality in rainfall is evident. At this latitude, the sun is directly overhead in May and again in September and does not rise more than 45° above the horizon on the winter solstice. Solar irradiance measured at the Bisley tower located 7 km to the east of the LFDP (visit <http://luq.lternet.edu> for description of methods used to measure rainfall and irradiance) reflects these seasonal changes in solar declination, exhibiting a broad peak between May and July and a trough between October and February (Figure 1a). Solar irradiance is 60% greater during peak months than during months around the winter solstice.

The Barro Colorado Forest Dynamics Plot (BCI; Condit *et al.* 1996) is located at 9°9'N, 79°51'W. Annual rainfall averages 2600 mm (measured with a Licor© 1400–106 tipping bucket, Nebraska) and is distributed

unevenly throughout the year so that just 10% falls during the dry season from January through April (Figure 1b). At this latitude, the sun is directly overhead in April and October; however, seasonal changes in cloud cover have an overwhelming impact on the amount of solar irradiance that reaches the forest (measured above the canopy with an LI200SA pyranometer, Licor©, Nebraska). In a comparison that controls solar declination, solar irradiance averages 31% greater on the March equinox, which falls in the relatively cloud-free dry season, than on the September equinox, which falls in the cloudy wet season (Wright & van Schaik 1994). Solar irradiance averages 48% greater during the 4-mo dry season than the 8-mo wet season on BCI (Figure 1b).

Data collection

Quantitative phenological records were collected at El Verde for 10 y and at BCI for 15 y using the same basic methodology. Flower and seed rain were monitored using 120 (El Verde) or 200 traps (BCI) placed in a stratified random manner with minimum distances of 15.7 m between traps. Trap surface area was 0.16 m² (40 cm on a side) and 0.5 m² (71 cm on a side), at El Verde and BCI, respectively. Traps at both sites were constructed using 1-mm-mesh window screen mounted 80–100 cm above the ground. Traps were censused every second week at El Verde beginning on 1 April 1992 except following Hurricane Georges when censuses were suspended from 21 September 1998 to 1 January 1999. There was probably little or no plant reproduction during this time period because the hurricane severely defoliated many trees. Traps were censused each week on BCI beginning on 1 January 1987. We analyse data collected at both sites through December 2002. These methods sample species which produce many small flowers or seeds (but seeds > 1 mm in diameter, the size of the mesh used) relatively well and species with very large flowers or seeds less well.

We defined flower records to be one or zero if flowers were present or absent, respectively, for each species, sampling date and trap. Seed production equalled the number of seeds captured plus the number of fruits captured multiplied by the mean number of seeds per fruit (Liogier 1985–1997, Wright & Calderón 1995). At El Verde we also tracked fertile fronds of one common species of epiphytic fern. All analyses were restricted to species encountered in at least 5% of the traps over the entire sampling period. This ensures that multiple individuals were sampled, as was verified on BCI by superimposing maps of the locations of traps that captured flowers and seeds and the locations of all large, potentially reproductive conspecifics for each tree species. This was

not verified at El Verde because the recent history of hurricane disturbance ensured small compact crowns on all trees. The difference in minimum trap numbers between sites (6 for El Verde vs. 10 for BCI) is justified by differences in the stature and average canopy size of the two forests (Brokaw *et al.* 2004). These data were further limited to species with a minimum number of 16 flowering or fruiting records. This minimum was required to detect non-annual flowering or fruiting patterns (see below). Nomenclature follows Liogier (1985–1997) and Correa (2004).

Quantification of species-level phenologies

Vector algebra was used to calculate mean flowering and fruiting dates for each species. Linear or Julian time scales fail when flowering and fruiting occur year-round. For example, if a single synchronous annual flowering event fell at the end of the year with similar numbers of flower records in December (mo = 12) and January (mo = 1), then the linear mean would fall in June (mo = 6.5). To avoid this problem, census dates were converted to an angle and weighted by the number of flower records or seeds to calculate mean vectors (see Batschelet 1981, pp. 7–18; and Wright & Calderón 1995 for additional details). The angle of the mean vector quantifies the mean date of flowering or fruiting. The length of the mean vector provides a measure of the temporal concentration. The length of the mean vector ranges from zero (when flowering or fruiting occurs uniformly throughout the year) to one (when flowering or fruiting is concentrated on the same sampling date each year).

Mean vectors fail for species with subannual (e.g., bimodal or multimodal) flowering or fruiting. For example, a species that flowered each March and each September (or in March of one year and September of another year) would have an arbitrary mean flowering date in June or December and a vector length near zero. To avoid this problem we conducted autocorrelation and contingency analyses to identify and exclude species with subannual flowering or fruiting patterns. The autocorrelation analyses of fortnightly (El Verde) and weekly (BCI) flowering and fruiting records used the entire 15-y record for BCI and the first 6.5 y before Hurricane Georges for El Verde. Species with a significant autocorrelation at a periodicity that was less than a multiple of 26 fortnightly or 52 weekly censuses were considered to be subannual for El Verde and BCI, respectively. The contingency analysis used monthly presence/absence data to identify species with multiple peaks or troughs in reproductive activity. The monthly data were pooled where necessary to maintain a minimum expected value of four for a

goodness of fit test (Batschelet 1981). Thus, analyses were for 1-mo, 2-mo or 3-mo intervals for species with ≥ 48 , 24–47 or 16–23 records, respectively. Species with < 16 records were excluded. Freeman–Tukey deviates were calculated for each cell (Sokal & Rohlf 1995, p. 750) and compared to a critical cut-off value ($\alpha = 0.05$), to detect significant peaks and troughs in flowering and fruiting. Bimodal species showed two or more significant peaks or troughs within a year. A sequential Bonferroni adjustment of the overall alpha of 0.05 was used to control Type I error (Rice 1989). Species with significant subannual phenologies were excluded from all mean vector calculations. Species that lacked any significant seasonality (either annual or non-annual) in the contingency analysis were considered to be aseasonal and were excluded from analyses involving mean vector angles (but not mean vector lengths).

To be able to include aseasonal and subannual species, we also defined the months of peak reproductive activity to include those months that comprised 75% of the records for each species for all sample years (Tables 2 and 3). That is to say, we calculated the percentage of flower records falling into each month, placed the months in rank order, and then recorded the months for which percentages summed to a minimum of 75%. We then summed the number of species exhibiting peak flower activity in each month to obtain a community-wide index of flowering seasonality that incorporates species with broad phenological peaks or subannual reproductive patterns. We repeated this calculation for seeds/fruits. Most species contributed to several monthly sums. This does not pose a problem for time series cross correlation analyses, which evaluate temporal dependence (Zar 1999). Mean vector angles, mean vector lengths, and numbers of species exhibiting peak activity were used to test the four hypotheses described in the Introduction.

We performed two tests to evaluate Hypotheses 1 and 2 (Hypothesis 2 is only relevant to BCI). The first was a contingency analysis to contrast numbers of species with mean dates of flowering or seedfall during seasons of high versus low irradiance (Hypothesis 1) or wet versus dry conditions (Hypothesis 2). These contingency analyses used log-likelihood analyses (G-tests, similar to a χ^2 -test; Sokal & Rohlf 1995) to evaluate the null expectation that an equal number of species would have mean dates in each month. For El Verde, months were combined into four periods corresponding to the May–July peak in irradiance, an August–September transition, the October–February trough in irradiance, and a March–April transition (Figure 1a). We predicted that deviations from the expected frequencies would be positive for May–July and negative for October–February for El Verde. For BCI, months were combined into three periods corresponding to the January–April

peak in irradiance, the May–August early wet-season trough in irradiance, and the September–December late wet-season trough in irradiance (Figure 1b). We divided the BCI wet season into two trimesters because we expected the impact of light limitation to be cumulative as the number of consecutive cloudy months increases even though irradiance is consistently low between May and December (Figure 1b). We therefore predicted that deviations from the expected frequencies would be positive in the first trimester, intermediate in the second trimester, and negative during the third trimester under Hypothesis 1 for BCI. We also predicted that deviations from the expected frequencies would be negative during the January–April dry season and positive during the two wet-season trimesters if moisture availability limits community-wide reproduction under Hypothesis 2 for BCI only. We used Freeman–Tukey deviates to identify significant cell deviations (Sokal & Rohlf 1995, p. 750).

The second test of Hypotheses 1 and 2 was a cross correlation analysis to evaluate relationships between the number of species exhibiting peak reproductive activity and monthly irradiance (Hypothesis 1) or monthly rainfall (Hypothesis 2) for lags of 1 to 11 mo. Because the data were circular in nature, we were able to conduct ‘wrap around’ lagged correlations. For example, for a lag of 1 mo we correlated mean irradiance for January with the number of species exhibiting peak reproductive activity for February, February with March, etc., and, finally, December with January. With respect to Hypothesis 1, we predicted that at both sites the number of species exhibiting peak reproductive activity would be positively related to irradiance for short lags if light levels limit community-wide reproduction. For Hypothesis 2, we predicted that the number of species exhibiting peak reproductive activity would be positively related to rainfall for short lags if moisture availability limits community-wide reproduction on BCI.

To test Hypothesis 3, seed development time was estimated from the difference in vector angles (mean dates) for flowering and fruiting. The mid-point of seed development was estimated using the circular mean of the flowering and fruiting dates. This mid-point was then used to assign the development time of each species to one of the site-specific time periods described under Hypothesis 1. A one-way ANOVA was conducted to determine whether development times differed among time periods.

To test Hypothesis 4, a contingency analysis was used to determine whether the monthly frequency of reproductive records differed between sites for each shared species. Where necessary, months with few records were combined to meet the minimum expected value of five observations per time period for a test of independence (Batschelet 1981).

RESULTS

Data availability and general attributes of reproductive phenologies

Five El Verde species and six BCI species exhibited significant bimodality in flowering or fruiting (Appendices 1 and 2). Ten of the 11 species exhibited bimodality only for flowering and not for fruiting, thus one flowering peak did not result in seed production. Bimodal species were subsequently removed from calculations involving vector algebra for reasons described under Methods. For El Verde, 58 and 64 species remained that were captured in 5% or more of the traps for flower and seed fall, respectively, and 51 of these species met this criterion for both phenophases so that fruit development times could be estimated. For BCI, there were 144 and 186 species for flower and seed fall, respectively, and 121 for which fruit development times could be estimated. As expected, small flowers and seeds/fruits were better sampled than were large flowers and seeds/fruit. For example, sample sizes were adequate for the small flowers but not the large seeds of *Andira inermis* (Appendix 1) and the small seeds but not the large flowers of *Ceiba pentandra* (Appendix 2).

At El Verde, the temporal concentrations of phenological activity (vector lengths) were relatively low, averaging 0.50 ± 0.03 (± 1 SE) and 0.57 ± 0.03 for flowering and fruiting, respectively (Figure 2b, f). At BCI, the temporal concentrations were consistently higher, averaging 0.71 ± 0.02 and 0.74 ± 0.02 for flowering and fruiting, respectively (Figure 3b, f). The distributions of vector lengths were strongly skewed for both phenophases at BCI such that concentrations of phenological activity exceeded 0.8 in most species. Three species lacked significant seasonality for each phenophase at each site (Figures 2 and 3). At El Verde, many species had mean flowering dates (Figure 2c) in the middle of the year with modes in March and August. Sums of the number of species in peak reproductive activity (Figures 2d, g) exhibited smoothed peaks near the middle of the year at El Verde, particularly for flowering. At BCI, the distributions of mean flowering and fruiting dates both had pronounced modes in March and April. Sums of the number of species in peak reproductive activity produced seasonal distributions similar to the distribution of mean phenological months for BCI (cf. Figures 3c vs. 3d and 3g vs. 3h).

Hypothesis 1: Reproductive activity is greatest during sunny seasons and lower during seasons of low irradiance

At El Verde, the number of species with mean dates in the four seasonal periods defined by levels of

Table 1. Log-likelihood (G) tests of contingency tables comparing the observed frequency of species flowering and fruiting to value expected on the assumption that species frequency were uniform throughout the year. Asterisks denote cells of contingency tables that exhibited a significant deviation from the expected frequency.

	Species flowering	Expected number	Species fruiting	Expected number
El Verde				
March–April	10	9.7	12	10.7
May–July	18	14.5	20	16
August–September	18*	9.7	14	10.7
October–February	12*	24.2	18	26.7
Total species	58		64	
G	13.2		5.15	
P	0.004		0.16	
Barro Colorado Island				
January–April	70*	48	85*	62
May–August	52	48	53*	62
September–December	22*	48	48*	62
Total species	144		186	
G	26.7		19.4	
P	< 0.0001		< 0.003	

irradiance differed significantly from the null expectation for flowering but not for fruiting (Table 1; $G = 13.2$, $P = 0.004$ and $G = 5.2$, $P = 0.16$, respectively). For flowering, there was a significant positive deviation from the expected frequency for the August–September transitional period and a significant negative deviation for the October–February irradiance trough. Thus, this first test of Hypothesis 1 provided partial support for our predictions for flowering but not for fruiting at El Verde. At BCI, the number of species with mean dates in the trimesters defined by levels of irradiance differed significantly from the null expectation for both flowering and fruiting (Table 1; $G = 26.7$, $P < 0.0001$ and $G = 12.4$, $P < 0.003$, respectively). For flowering, there was a significant positive deviation for the dry season (January–April) and a significant negative deviation for the late wet season (September–December). For fruiting, there was a significant positive deviation in the dry season and significant negative deviations for both the early and late wet seasons. Community-level flowering and fruiting patterns at BCI conform to Hypothesis 1.

We also examined cross correlations between mean monthly irradiance and the number of species exhibiting peak reproductive activity in each month. Peak reproductive activity was defined to include the fewest months that comprised 75% or more of the flower records or seeds captured for each species (Figures 2d, h and 3d, h). At El Verde, the numbers of species in peak flowering (Figure 2d) ranged from 19 in February to 38 in August and included a broad peak that extended from May through September. Cross correlations with mean monthly irradiance were strongly positive for lags of 0

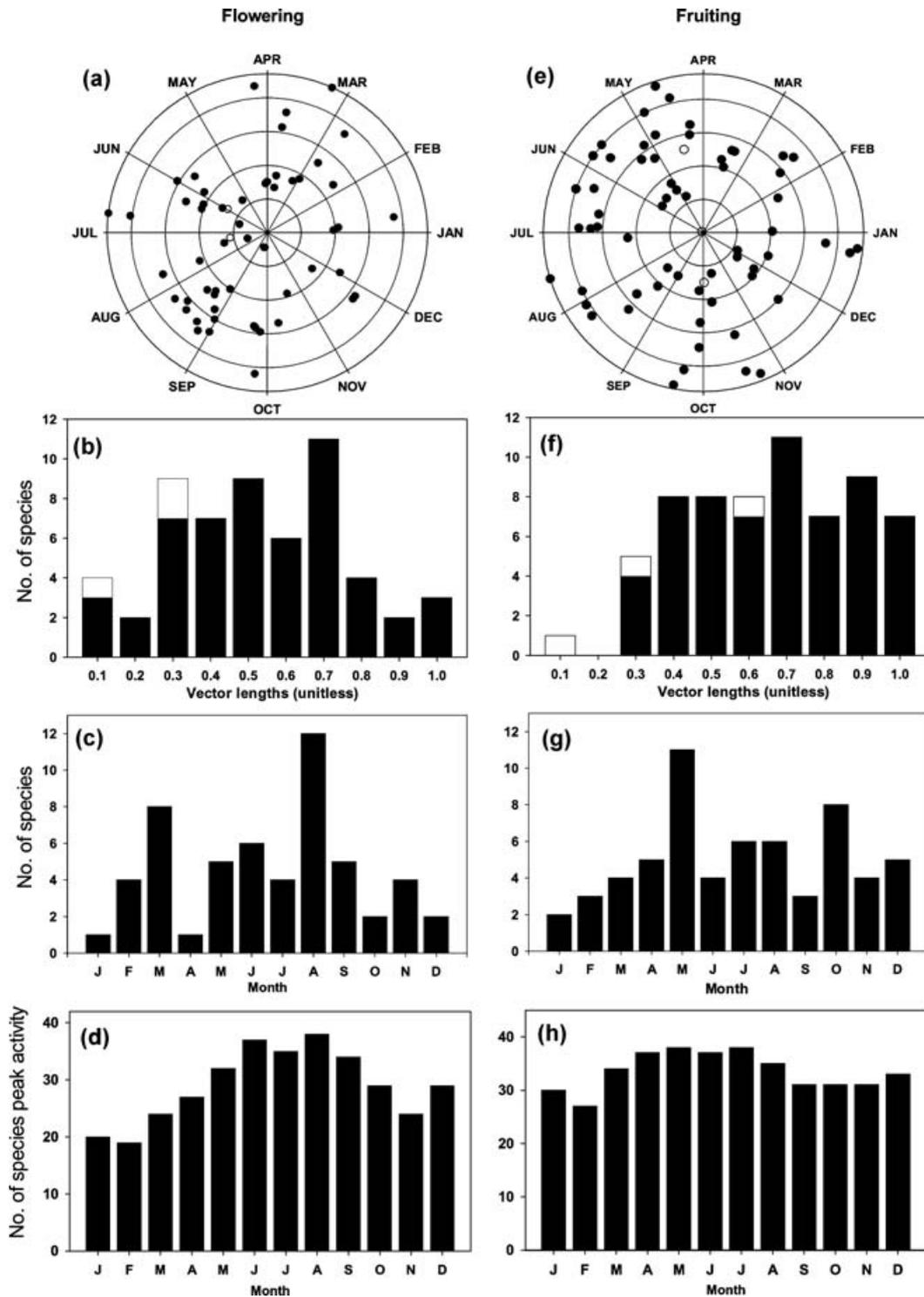


Figure 2. Phenologies of flower (left column of panels) and seed production (right column) at El Verde. The upper panels (a, e) present polar plots of mean vectors, where vector angles represent mean dates and vector lengths represent temporal concentrations. Vector lengths scale between zero when the activity is equally likely on all dates and one when the activity occurs on a single date each year. The second row of panels (b, f) presents histograms of numbers of species for temporal concentration. Closed and open symbols represent species with and without significant seasonality, respectively. The third row of panels (c, g) presents histograms of numbers of species for mean dates, ignoring species with non-significant seasonality. The bottom row of panels (d, h) shows community-wide peak months of reproductive activity. This community-wide metric equals the number of species for which the month was included among the months that cumulatively accounted for 75% of annual reproductive output for a particular species (Appendix 1).

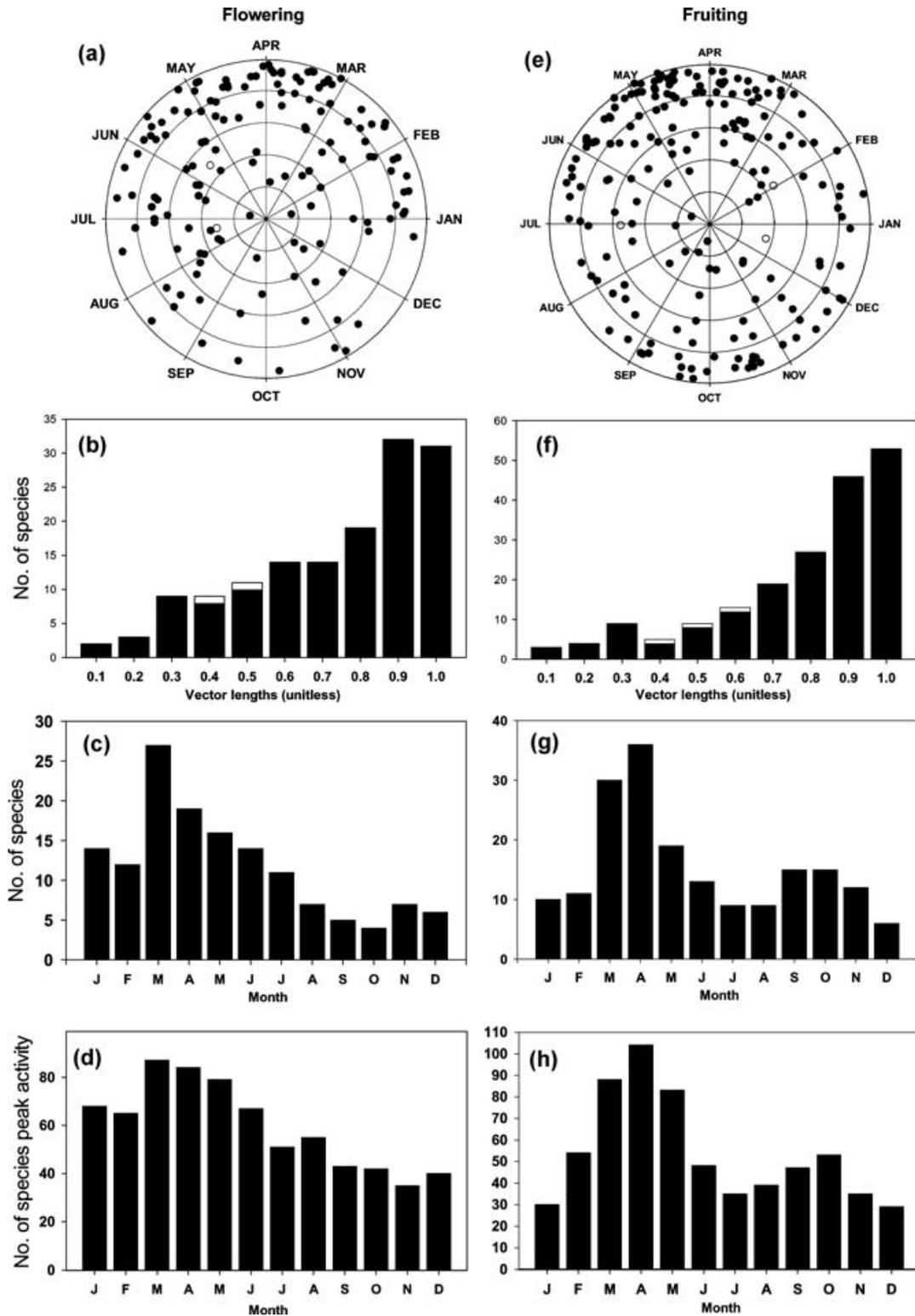


Figure 3. Phenologies of flower (left column of panels) and seed production (right column) at the Barro Colorado Island Forest Dynamics plot. The caption to Figure 2 explains each panel.

to 4 mo and negative for lags of 6 to 9 mo (Figure 4a). Thus, the timing of peak flowering is consistent with the light limitation hypothesis at El Verde. The number

of species in peak fruiting (Figure 2h) only ranged from 27 in February to 38 in May and again in July with a shallow peak from March through August and a second,

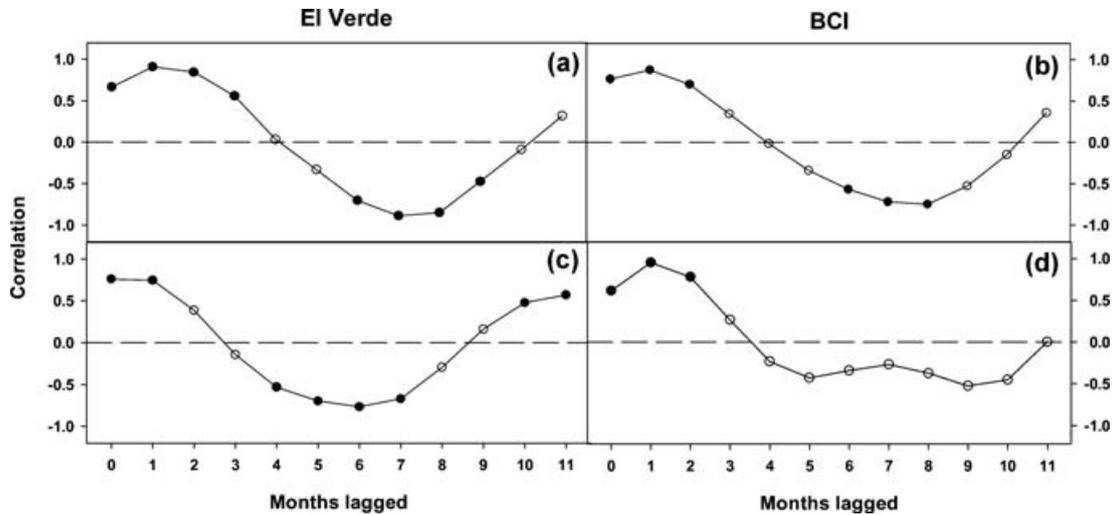


Figure 4. Lagged correlations of flowering and fruiting activity at El Verde and BCI (summed number of species per month falling in the months containing 75% of annual activity for a species) with mean monthly irradiance. Panels are: flowering at El Verde (a), flowering at BCI (b), fruiting at El Verde (c), and fruiting at BCI (d).

short peak in December and January. Cross correlations with mean monthly irradiance were positive for lags of 0 and 1 mo and negative for lags of 4 to 7 mo (Figure 4b). Thus, the timing of fruiting is also consistent with the light limitation hypothesis at El Verde even though there was limited variation in the number of species exhibiting peak fruiting among months.

The cross correlation analyses also supported the hypothesis that light availability determines the community-wide timing of flowering and fruiting at BCI (Figure 4c, d). The number of species in peak flowering (Figure 3d) ranged from 35 in November to 87 in March. Cross correlations with mean monthly irradiance were strongly positive at lags of 0 to 3 mo and negative for lags of 6 to 8 mo (Figure 4c). The numbers of species exhibiting peak fruiting (Figure 3h) ranged from 29 in December and January to 104 in April. Cross correlations with irradiance were strongly positive at lags of 0 to 2 mo and negative at a lag of 9 mo (Figure 4d). The cross correlation analyses support the hypothesis that light availability determines the community-wide timing of flowering and fruiting on BCI.

Hypothesis 2: Reproductive activity is greatest during the rainy season and lower during the dry season when moisture availability limits plant function

Hypothesis 2 was only evaluated for BCI because moisture is not seasonally limiting at El Verde. The number of species with mean flowering dates and mean fruiting dates in the dry season were both significantly greater than expected (Table 1). The number of species with mean

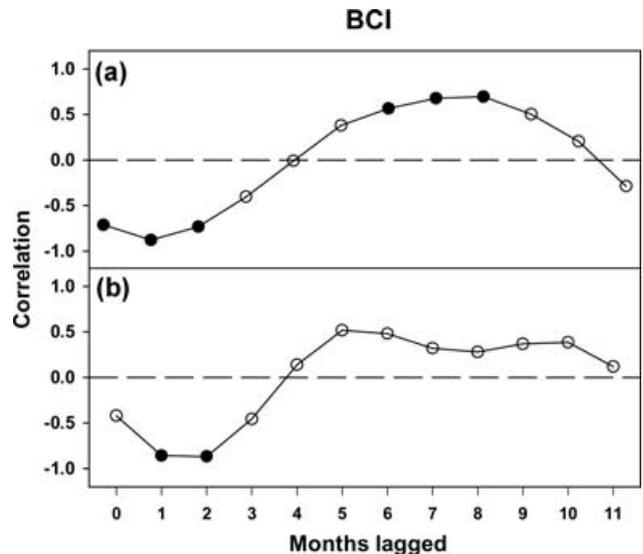


Figure 5. Lagged correlations of flowering (a) and fruiting activity (b) at BCI (summed number of species per month falling in the months containing 75% of annual activity for a species) with mean monthly rainfall.

flowering dates in the second half of the wet season was significantly lower than expected (Table 1). The number of species with mean fruiting dates was significantly lower than expected for both the first and second halves of the wet season (Table 1). This precisely contradicts predictions based on the moisture limitation hypothesis. The cross correlation analyses produced similar results. The number of species exhibiting peak flowering activity was negatively correlated with mean monthly rainfall for lags of 0 to 3 mo (Figure 5a). Likewise, the number of

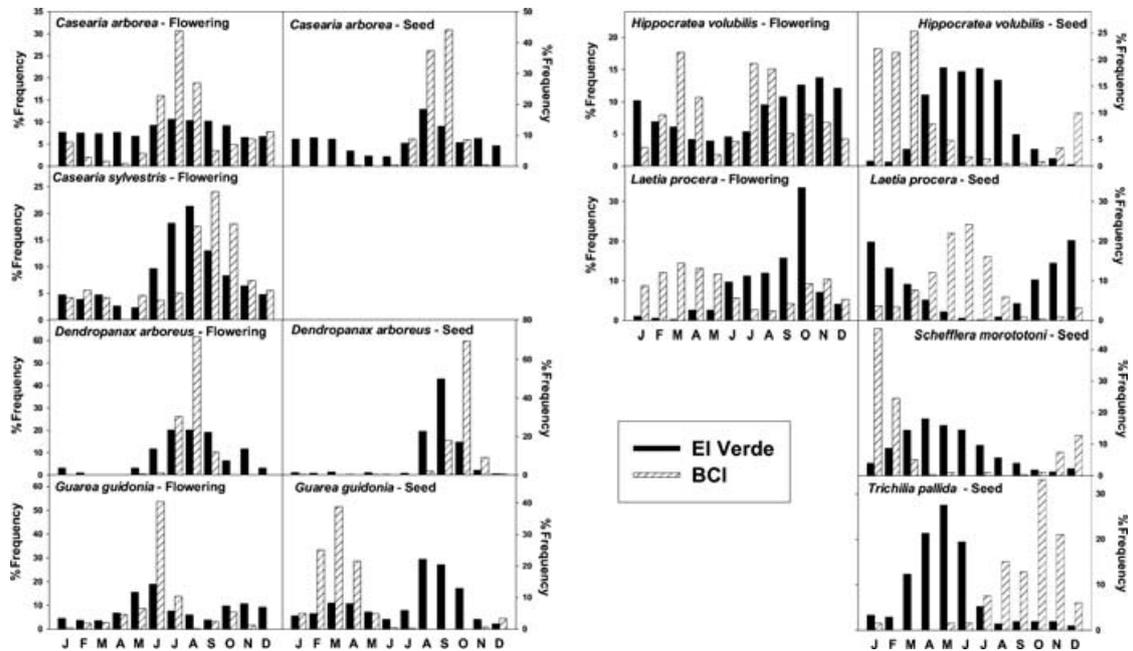


Figure 6. Seasonality of phenologies for eight species occurring at both El Verde and BCI. Data are monthly per cent frequency of total flowering or fruiting (number of seeds) within a site.

Table 2. Fruit development time (mo) (mean \pm SE), estimated from the difference in mean month of flowering and fruiting, in relation to time of year in which the period of fruit production was centred.

Time of year	Fruit development time (mo)
El Verde	
March–April	3.35 \pm 1.01
May–July	3.22 \pm 0.78
August–September	2.66 \pm 0.69
October–February	5.82 \pm 0.79
Barro Colorado Island	
January–April	2.36 \pm 0.20
May–August	3.07 \pm 0.29
September–December	4.89 \pm 0.55

species exhibiting peak fruiting activity was negatively correlated with mean monthly rainfall for lags of 2 and 3 mo (Figure 5b). The hypothesis that moisture availability determines the timing of community-wide reproductive activity on BCI is consistently rejected.

Hypothesis 3: Irradiance influences seed development time

We predicted that fruit development times would be shorter during periods of high irradiance and longer during periods of low irradiance. Fruit development times were quantified as the difference between the mean month of flowering and the mean month of fruiting for each species. At El Verde, fruit development times differed significantly among the four seasonal periods defined by irradiance ($F_{3,47} = 3.07$, $P = 0.037$). Development

times averaged 5.82 mo during the October–February irradiance trough and approximately 3 mo for the three sunnier time periods (Table 2). At BCI, fruit development times also varied significantly among the trimesters defined by irradiance ($F_{2,118} = 14.8$, $P < 0.0001$). Development times averaged 2.36 mo during the sunny dry season and 4.89 mo in the late wet season when cloudy conditions had already prevailed for the previous 4–8 mo (Table 2). The data are consistent with the hypothesis that irradiance influences fruit development times at both sites.

Hypothesis 4: Shared species

Eight species present at both El Verde and BCI allowed us to evaluate Hypothesis 4. Evidence supported Hypothesis 1 and not Hypothesis 2. Therefore, if these shared species followed the overall community patterns, the same species should concentrate flowering and fruiting near the summer solstice at El Verde and in the dry season at BCI. On the other hand, if phenologies are evolutionarily fixed and conditions favourable for reproduction set an ecological filter on geographic distributions, then the shared species should flower and fruit in the wet season at BCI and at the same time at El Verde.

The reproductive phenologies of all shared species differed significantly between sites ($P < 0.0001$, Figure 6). The contingency analysis is sensitive to any difference in temporal distributions between sites, not just those

differences related to our hypothesis. For example, as observed previously (Figures 2 and 3), individual species flower and fruit for longer periods at El Verde than at BCI and this is also true for several shared species including *Casearia arborea* (both phenophases) and *Schefflera morototoni* (fruiting). We rely on inspection to further evaluate the fourth hypothesis. Four species exhibit strong differences in phenology between sites. Fruiting of *Hippocratea volubulis* and flowering in *Laetia procera* appear to conform to the prediction of convergence on the local community-wide pattern, but bimodal flowering in both species at BCI complicates comparisons. In none of the remaining comparisons does a species flower or fruit in the summer months at El Verde and in the dry season on BCI (Figure 6). For four species, *Casearia arborea*, *C. sylvestris*, *Dendropanax arboreus* and *Guarea guidonia*, the timing of phenological activities is qualitatively similar between sites and they flower in the wet season on BCI and in the summer at El Verde (Figure 6). These four species are consistent with the hypothesis that reproductive phenologies are evolutionarily stable and conditions favourable for reproduction set an ecological filter on geographic distributions.

DISCUSSION

The timing of flowering and fruiting

Community-wide peaks and troughs in the number of species flowering and fruiting track seasonal variation in irradiance for both sites, suggesting that this component of seasonality has been an important factor shaping the evolution of phenologies at both sites. At El Verde, average irradiance is 60% greater near the summer solstice than near the winter solstice (Figure 1a). The number of species with mean flowering dates near the winter solstice is significantly smaller than expected by chance (Table 1), and both the number of species in peak flowering and peak fruiting are significantly and positively correlated with monthly mean irradiance for the current and the previous month (Figure 4a, c). Also at El Verde, understorey plants of eight tree and shrub species show distinct peaks of leaf flush in May and June, which is consistent with the hypothesis that the timing of leaf flush also has evolved in response to seasonal variation in irradiance (Angulo-Sandoval & Aide 2000, Angulo-Sandoval *et al.* 2004).

At BCI, irradiance averages 48% greater during the sunny, 4-mo dry season than during the cloudy, 8-mo wet season (Figure 1b). The number of species with mean flowering and fruiting dates in the sunny dry season is significantly greater than expected by chance (Table 1), the number of species with mean flowering and fruiting dates in the cloudy wet season and in particular

in the second half of the wet season is significantly smaller than expected by chance (Table 1), and both the number of species in peak flowering and peak fruiting are significantly and positively correlated with monthly mean irradiance for the current and the previous two months (Figure 4b, d). The timing of community-wide peaks and troughs in numbers of flowering and fruiting species also directly contradicts the hypothesis that moisture availability evolutionarily limits reproduction in the seasonal forests of BCI. Both flowering and fruiting reached peak levels in the dry season and especially in the late dry season when moisture is most limiting (Figures 3, 5). Positive cross correlations between mean monthly irradiance and number of species in peak flower and fruit production for lags of 0 to 3 mo (Figure 4) also support the conclusion that community-wide peaks in flowering and fruiting coincide with the seasons of greatest irradiance in both the aseasonal forests of El Verde and the seasonal forests of BCI.

Fruit development times

In addition to affecting the community-wide timing of flowering or fruiting, seasonal variation in irradiance also had a significant impact on the time required for fruit development. We estimated fruit development time by subtracting the mean fruiting times from mean flowering times at both sites. At El Verde, fruit development times averaged just 3 mo for species fruiting at sunnier times of year, but were almost 6 mo for species fruiting between October and February, near the winter solstice (Table 2). Similarly, on BCI, fruit development times averaged just 2.3 mo during the sunny dry season (January–April), 3 mo during the early wet season (May–August), and almost 5 mo during the late wet season (September–December). The difference in mean fruit development time between the early and late wet season on BCI, periods of similar average irradiance levels, suggests that additional unidentified factors also influence the evolution of fruit development time.

Fruit development times calculated separately for each species averaged considerably longer than the difference between the community-wide peaks in numbers of species at peak flowering and fruiting (cf, Table 2 and Figures 2d, h and 3d, h). This apparent difference is easily reconciled. The summed numbers of species characterized by peak flowering and fruiting weighs a number of months equally for each species. This weighting minimizes large differences in fruit development times, because, in a given species, both flowering and fruiting records tend to peak quickly soon after the first flowers and fruits appear and then decline slowly (Wright & Calderon 2006).

While the long fruit development time of species initiating fruits at the beginning of seasonally low irradiance conforms to our hypothesis, it may,

nevertheless, also be adaptive for other reasons. On BCI, some of the long development times place seeds on the forest floor at the onset of seasonal rains or, in combination with delayed germination (Garwood 1983), ensures that seeds do not germinate until soil moisture is adequate to support germinating seedlings. A similar argument may apply to some species at El Verde (which probably do not exhibit dormancy – this is unlikely in an ever-wet forest; Everham *et al.* 1996, Garwood 1989). For example, many late-flowering species with long fruit development times (e.g. *Drypetes glauca*, *Ocotea* species, *Palicourea riparia*; Appendix 1) have mean seed production dates in May, a time when light levels in the understorey, which might be critical for early seedling establishment, are approaching their seasonal peak. Variation in fruit development time together with the timing of seed dispersal, dormancy, seed size, and other seed and seedling traits might combine to permit germination at optimal times while minimizing the collective impact of predators and pathogens which attack developing fruit, seeds in the soil seed bank, and seedlings comprising a seedling bank (Garwood 1989, Greig 1993, Maron & Gardner 2000, Moles *et al.* 2003).

Shared species

Eight species present at both El Verde and BCI allowed us to determine whether reproductive phenologies were conservative or plastic, and, if plastic, whether the timing of reproduction converged on the local community-wide pattern at each site. Four of the eight species reproduced at different times at BCI and El Verde and failed to converge on the local community-wide pattern at one site (Figure 6, *Hippocratea volubulis* and *Laetea procera*) or both sites (Figure 6, *Schefflera morototoni* and *Trichilia pallida*). The four remaining species flowered in the wet season on BCI and during the same months at El Verde (Figure 6, left column) suggesting that phenologies are evolutionarily conservative in these four species and, in addition, that conditions appropriate for reproduction establish an ecological filter that limits geographic distributions (Kochmer & Handel 1986).

Physiological limitation versus ultimate selection for the timing of reproduction

Our approach in this study has been to assemble a large collection of species-level data at a seasonal and an aseasonal site and then to determine whether there is a strong signature of either rainfall or irradiance seasonality on community-level patterns of flowering and fruiting for each site. At both sites, fruit development times and the timing of both peaks and troughs of community-wide flowering and fruiting all track seasonal variation in irradiance. These community-wide patterns might

reflect ongoing physiological limitation of reproduction by light availability as well as past selection for phenologies to match the season of greatest light availability. The four shared species with similar timing of flowering and fruiting at both sites suggest that past selection for relatively conservative reproductive phenologies has been more important. The additional observation that El Niño events bring unusually high levels of light availability to BCI during the normally cloudy wet season and that this leads to greater flower and seed production but not to changes in timing (Wright & Calderón 2006) further suggests that the timing of reproduction has been selected to coincide with the seasonal peak in light availability. A more complete understanding of the causes of the seasonal patterns documented here will await new studies of factors that limit growth by tropical forest plants, the proximate cues for flowering, and their plasticity and heritability.

The importance of light availability for the timing of reproduction is likely to vary with moisture availability. This is nicely illustrated in tropical dry forests where riparian species with year-round access to water reproduce at the time of peak irradiance and upland species that experience relatively severe dry-season drought reproduce near the onset of seasonal rains (Borchert 1994, Wright & van Schaik 1994). At BCI, our more seasonal site, annual rainfall averages 2600 mm and monthly rainfall averages 29–90 mm during the 4-mo dry season. We expect that seasonal changes in moisture availability will have a greater impact on the timing of flowering and fruiting in drier forests where the dry season is longer and/or more severe.

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Appendix 1. Summary of phenological data collected in the Luquillo Forest Dynamics Plot from April 1992 to December 2002 (excluding late September–December 1998) including all species/phenophases represented by ≥ 6 traps and ≥ 16 total observations. Life forms are coded as E = epiphyte, H = hemiepiphyte, L = large tree, Li = Liana, m = medium tree, P = hemiparasite, S = small tree, Sh = shrub and V = vine. Flowering was measured as the number of traps that contained at least one flower of a particular species on a particular date. Fruiting was recorded as the number of seeds in a trap for a particular species and date plus the number of fruit multiplied by the mean number of seeds per fruit for that species. In addition to the mean month of phenological activity and mean vector, the fewest months comprising at least 75% of observations are included to show dispersion of values (1 = January, 2 = February, etc.).

Species	Family	Life form	Flowering					Seeds				
			No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.	No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.
<i>Alchornea latifolia</i>	Euphorbiaceae	L	65	531	3.7	0.63	2–5	41	357	5.6	0.80	4–7, 9
<i>Alchorneopsis floribunda</i>	Euphorbiaceae	M	48	295	– ¹	– ¹	2, 3, 6–10, 12	80	14174	9.8	0.69	7–12
<i>Andira inermis</i>	Fabaceae	L	19	135	7.6	0.66	6–9	–	–	–	–	–
<i>Buchenavia capitata</i>	Combretaceae	L	78	936	6.0	0.61	3–7	9	28	9.9	0.30	1–4, 8–10, 12
<i>Byrsonima spicata</i>	Malpighiaceae	M	75	1071	8.4	0.66	6–9	27	562	12.6	0.88	1, 11, 12
<i>Casearia arborea</i>	Flacourtiaceae	M	117	5627	9.6	0.09	1, 2, 6–12	99	15000	10.3	0.25	1–3, 7–12
<i>Casearia sylvestris</i>	Flacourtiaceae	M	96	1211	8.8	0.40	6–11	53	5453	8.6	0.42	3, 7–10
<i>Cecropia schreberiana</i>	Cecropiaceae	M	26	186	2.2	0.48	1–3, 5, 11, 12	120	37212	4.3	0.59	1–6, 11, 12
<i>Chionanthus domingensis</i>	Oleaceae	M	63	596	4.2	0.87	3–5	27	114	8.0	0.82	5–9
<i>Cissampelos pareira</i>	Menispermaceae	V	–	–	–	–	–	19	97	8.9	0.30	1, 2, 5, 7–12
<i>Cissus sicyoides</i>	Vitaceae	V	12	24	6.7	0.81	5–7	19	47	7.8	0.80	3, 7–9
<i>Clibadium erosum</i>	Asteraceae	Sh	15	20	3.2	0.94	2, 3	–	–	–	–	–
<i>Clusia gundlachii</i>	Clusiaceae	H	9	103	9.5	0.09	1, 5, 6, 8–12	60	251	5.1	0.30	2–8, 10, 12
<i>Clusia rosea</i>	Clusiaceae	H	–	–	–	–	–	18	36	8.2	0.83	5–8
<i>Cordia borinquensis</i>	Euphorbiaceae	S	21	223	7.6	0.19	4–10, 12	7	35	6.9	0.63	4–9
<i>Cordia sulcata</i>	Boraginaceae	M	–	–	–	–	–	7	16	9.0	0.78	4, 5, 8, 9, 10
<i>Croton poecilanthus</i>	Euphorbiaceae	M	38	765	6.4	0.17	3–12	15	112	5.5	0.30	1, 3–8, 10, 12
<i>Dacryodes excelsa</i>	Burseraceae	L	112	5583	9.6	0.57	7–11	91	1612	9.8	0.54	1, 7–12
<i>Dendropanax arboreus</i>	Araliaceae	M	31	93	8.8	0.60	6–9, 11	56	3862	9.5	0.93	8–10
<i>Dioscorea polygonoides</i>	Dioscoreaceae	V	17	27	6.0	0.30	1, 3–6, 11	36	222	11.7	0.37	1, 2, 4–6, 8–12
<i>Drypetes glauca</i>	Euphorbiaceae	S	25	114	8.3	0.62	6–9	22	78	5.7	0.71	3–8
<i>Eugenia stahlii</i>	Myrtaceae	M	8	34	9.7	0.84	8, 9, 10	–	–	–	–	–
<i>Ficus trigonata</i>	Moraceae	H	13	43	11.9	0.49	1, 5, 9–12	48	17549	10.1	0.42	1, 7–12
<i>Forsteronia portoricensis</i>	Apocynaceae	V	60	879	8.7	0.55	6–10	–	–	–	–	–
<i>Gonzalagunia spicata</i>	Rubiaceae	Sh	10	67	10.5	0.38	4, 8–12	–	–	–	–	–
<i>Guarea glabra</i>	Meliaceae	S	11	27	5.9	0.27	1, 5–7, 11	–	–	–	–	–
<i>Guarea guidonia</i>	Meliaceae	L	88	1167	– ¹	– ¹	4–7, 10–12	89	652	9.8	0.35	2–5, 7–11
<i>Guettarda valenzuelana</i>	Rubiaceae	M	10	113	8.9	0.68	7–10	19	38	11.5	0.60	1, 6, 8–12
<i>Guzmania</i> sp.	Bromeliaceae	E	–	–	–	–	–	91	584	4.2	0.65	1–6
<i>Heteropteris laurifolia</i>	Malpighiaceae	Li	32	152	9.6	0.56	7–10, 12	36	391	10.5	0.87	9–12
<i>Hippocratea volubilis</i>	Hippocrateaceae	Li	99	2493	11.5	0.34	1, 2, 8–12	70	840	6.6	0.63	4–9
<i>Hirtella rugosa</i>	Chrysobalanaceae	S	25	191	3.2	0.34	1–5, 11, 12	16	34	4.8	0.24	2, 4–7, 11, 12
<i>Homalium racemosum</i>	Flacourtiaceae	L	88	1755	8.6	0.67	7–10	65	4865	9.6	0.83	7–10
<i>Inga laurina</i>	Fabaceae	M	113	2166	– ¹	– ¹	3, 5, 8–12	12	30	2.3	0.70	1–3, 10
<i>Inga vera</i>	Fabaceae	M	38	296	– ¹	– ¹	2–5, 7–10	–	–	–	–	–

Appendix 1. Continued.

Species	Family	Life form	Flowering					Seeds				
			No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.	No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.
<i>Ipomoea setifera</i>	Convolvulaceae	V	32	156	2.8	0.74	1–3	–	–	–	–	–
<i>Ipomoea tiliacea</i>	Convolvulaceae	V	64	1674	4.1	0.29	1–8	29	197	5.9	0.29	2–9
<i>Ixora ferrea</i>	Rubiaceae	S	47	178	10.1	0.54	8–12	9	228	4.4	0.51	1, 3–6, 11, 12
<i>Laetia procera</i>	Flacourtiaceae	L	79	377	9.7	0.59	6–10	108	3329	12.7	0.73	1–3, 10–12
<i>Macfadyena unguis-cati</i>	Bignoniaceae	Li	–	–	–	–	–	7	35	4.9	0.80	3–6
<i>Mamillara bidentata</i>	Sapotaceae	L	71	737	8.4	0.49	6–10, 12	40	122	2.5	0.66	1–4, 6, 10, 12
<i>Margaritaria nobilis</i>	Euphorbiaceae	M	6	26	6.7	0.94	6, 7	23	194	10.6	0.91	9–11
<i>Marcgravia rectiflora</i>	Margraviaceae	V	75	1073	3.0	0.37	1–5, 11, 12	54	17821	6.9	0.74	4–8
<i>Matayba domingensis</i>	Sapindaceae	M	76	1177	3.7	0.72	2–5	48	300	6.3	0.80	4–7
<i>Miconia racemosa</i>	Melastomataceae	Sh	20	40	5.9	0.44	1, 4–6, 8	8	88	8.5	0.64	4, 6–10, 12
<i>Mikania fragilis</i>	Asteraceae	V	–	–	–	–	–	72	553	4.5	0.83	3–6
<i>Myrcia leptoclada</i>	Myrtaceae	S	–	–	–	–	–	17	30	12.2	0.41	1, 6, 7, 11, 12
<i>Myrcia splendens</i>	Myrtaceae	S	15	24	7.2	0.22	3, 4, 6, 8, 9	13	18	12.6	0.92	1, 11, 12
<i>Neuradophia volubilis</i>	Fabaceae	V	9	45	11.6	0.64	1, 10–12	–	–	–	–	–
<i>Ocotea leucoxydon</i>	Lauraceae	M	36	188	8.5	0.48	6–9, 11	22	184	2.3	0.58	1–4, 10–12
<i>Ocotea sintenisii</i>	Lauraceae	M	24	107	11.6	0.64	10–12	46	197	4.6	0.92	3–5
<i>Ormosia krugii</i>	Fabaceae	M	10	38	1.2	0.75	1, 2, 12	–	–	–	–	–
<i>Palcourea riparia</i>	Rubiaceae	Sh	50	475	12.9	0.39	1, 2, 5, 9–12	40	734	5.1	0.63	2–7, 11
<i>Paullinia pinnata</i>	Sapindaceae	Li	74	505	8.7	0.71	7–10	12	33	1.8	0.49	1–3, 7, 9, 11, 12
<i>Phoradendron piperoides</i>	Loranthaceae	P	10	36	4.0	0.30	3–6, 9, 12	46	611	3.5	0.45	1–5, 8, 10–12
<i>Phytolacca rivinoides</i>	Phytolaccaceae	Sh	–	–	–	–	–	61	335	6.1	0.01	1, 3–9, 10, 12
<i>Piper glabrescens</i>	Piperaceae	Sh	–	–	–	–	–	47	1232	3.5	0.41	1, 3–6, 11, 12
<i>Polypodium piloselloides</i> ²	Polypodiaceae	E	–	–	–	–	–	54	7508	3.3	0.52	1–6, 11, 12
<i>Prestoea montana</i>	Arecaceae	M	101	3448	7.4	0.26	3–10	116	4919	1.0	0.41	1–4, 8–12
<i>Psychotria berteriana</i>	Rubiaceae	S	58	470	2.8	0.51	1–5, 12	85	5144	5.8	0.80	4–7
<i>Psychotria brachiata</i>	Rubiaceae	Sh	24	87	7.7	0.43	4, 6–9, 12	51	2158	11.7	0.25	1, 4, 6, 9–12
<i>Rourea surinamensis</i>	Connaraceae	Li	116	4264	– ¹	– ¹	4–7, 10–12	102	1990	5.1	0.35	1–3, 5–7, 11, 12
<i>Roystonea borinquena</i>	Arecaceae	L	13	153	3.7	0.34	1–6, 12	59	182	11.5	0.39	1, 2, 7–12
<i>Sapium laurocerasum</i>	Euphorbiaceae	M	24	153	5.2	0.24	2–8	69	956	7.1	0.45	3, 5–10
<i>Schlegelia brachyantha</i>	Bignoniaceae	V	61	841	3.7	0.27	1–6, 8, 12	83	1780	3.4	0.52	1–5, 7, 8, 10, 12
<i>Schefflera morototoni</i>	Araliaceae	M	40	366	12.9	0.42	1–3, 10–12	113	7064	5.1	0.53	1–8
<i>Securidaca virgata</i>	Polygalaceae	V	52	476	6.2	0.51	4–8	58	348	8.4	0.54	5–12
<i>Sloanea berteriana</i>	Elaeocarpaceae	L	63	443	7.5	0.12	1, 5–8, 10, 12	27	110	11.9	0.23	2–6, 10, 11
<i>Smilax domingensis</i>	Smilacaceae	V	81	450	8.1	0.67	6–9	32	271	5.3	0.57	1–8
<i>Solanum rugosum</i>	Solanaceae	Sh	–	–	–	–	–	7	460	7.5	0.95	7, 9
<i>Solanum torvum</i>	Solanaceae	Sh	–	–	–	–	–	10	24	8.4	0.30	2, 7–9
<i>Tabebuia heterophylla</i>	Bignoniaceae	M	22	303	5.7	0.54	3–6, 10	80	5188	6.9	0.67	5–7, 11, 12
<i>Tetragastris balsamifera</i>	Burseraceae	L	26	128	6.2	0.41	4–9	24	110	6.2	0.70	3–8
<i>Trichilia pallida</i>	Meliaceae	M	69	397	8.5	0.46	6–9, 11, 12	47	205	4.9	0.65	2–6, 11
<i>Zanthoxylum martinicense</i>	Rutaceae	L	9	65	6.3	0.41	4–8	–	–	–	–	–

¹Mean month and vector cannot be calculated because the species exhibits significant bimodality.²Fertile fronds were counted for this fern species.

Appendix 2. Summary of phenological data collected in the Barro Colorado Island Forest Dynamics Plot from January 1987 to December 2002 including all species/phenophases represented by ≥ 10 traps and ≥ 16 total observations. Life forms are coded as E = epiphyte, H = hemiepiphyte, L = large tree, Li = Liana, m = medium tree, P = hemiparasite, S = small tree, Sh = shrub and V = vine. Flowering was measured as the number of traps that contained at least one flower of a particular species on a particular date. Fruiting was recorded as the number of seeds in a trap for a particular species and date plus the number of fruit multiplied by the mean number of seeds per fruit for that species. In addition to the mean month of phenological activity and mean vector, the fewest months comprising at least 75% of observations is included to show dispersion of values (1 = January, 2 = February, etc.).

Species	Family	Life form	Flowering					Seeds				
			No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.	No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.
<i>Acacia hayesii</i>	Fabaceae	Li	37	660	10.8	0.90	10, 11	31	230	4.6	0.95	4, 5
<i>Adelia triloba</i>	Euphorbiaceae	Sh	20	273	1.5	0.91	1, 2, 12	–	–	–	–	–
<i>Aegiphila cephalophora</i>	Verbenaceae	Li	13	261	8.6	0.66	7, 8, 11	62	660	11.6	0.91	11, 12
<i>Alchornea costaricensis</i>	Euphorbiaceae	S	21	343	4.9	0.84	3–5	63	22687	6.4	0.92	5–7
<i>Allophylus psilospermus</i>	Sapindaceae	S	–	–	–	–	–	17	36	7.7	0.82	7
<i>Alseis blackiana</i>	Rubiaceae	S	89	921	5.1	0.96	4, 5	189	1487718	4.5	0.83	1–7, 12
<i>Amphilophium paniculatum</i>	Bignoniaceae	Li	13	254	11.3	0.88	10, 11	47	482	3.4	0.83	2–4
<i>Anacardium excelsum</i>	Anacardiaceae	L	27	2127	3.8	0.84	2–4	38	635	4.9	0.93	4, 5
<i>Annona spraguei</i>	Annonaceae	M	–	–	–	–	–	39	7632	9.7	0.97	9, 10
<i>Anthodon panamense</i>	Hippocrateaceae	Li	51	1432	9.5	0.23	6–8, 10–12	43	276	9.5	0.42	5, 7–11
<i>Apeiba membranacea</i>	Tiliaceae	L	45	2456	7.3	0.48	4–9	43	36229	3.0	0.92	2, 3
<i>Apeiba tibourbou</i>	Tiliaceae	L	14	171	10.3	0.40	1, 8–12	–	–	–	–	–
<i>Arrabidaea candicans</i>	Bignoniaceae	Li	25	187	12.8	0.81	1, 9, 12	55	285	4.8	0.80	3–5
<i>Arrabidaea chica</i>	Bignoniaceae	Li	29	181	11.5	0.58	1, 9, 10, 12	39	170	4.1	0.86	3, 4
<i>Arrabidaea florida</i>	Bignoniaceae	Li	–	–	–	–	–	18	79	4.8	0.90	4, 5
<i>Arrabidaea patellifera</i>	Bignoniaceae	Li	30	599	8.3	0.55	6–10	34	1293	3.3	0.84	2, 3
<i>Arrabidaea verrucosa</i>	Bignoniaceae	Li	41	211	7.1	0.70	6, 7, 12	53	295	11.2	0.32	2–4, 10, 12
<i>Aspidosperma spruceanum</i>	Apocynaceae	L	–	–	–	–	–	10	35	5.5	0.76	3, 5, 6
<i>Astrocaryum standleyanum</i>	Arecaceae	S	–	–	–	–	–	13	88	4.6	0.49	3–5, 10, 11
<i>Astronium graveolens</i>	Anacardiaceae	L	28	421	3.3	0.90	2, 3	22	105	4.9	0.99	4
<i>Banisteriopsis cornifolia</i>	Malpighiaceae	Li	33	154	1.3	0.88	1, 12	11	27	3.5	0.67	2, 3, 5
<i>Beilschmiedia pendula</i>	Lauraceae	L	43	797	12.8	0.93	1, 12	81	1162	5.8	0.92	5, 6
<i>Brosimum alicastrum</i>	Moraceae	L	27	1939	5.4	0.38	2–8	107	8563	6.6	0.88	5–7
<i>Callichlamys latifolia</i>	Bignoniaceae	Li	32	108	1.0	0.46	1, 4, 5, 10–12	29	130	3.8	0.89	3, 4
<i>Calophyllum longifolium</i>	Clusiaceae	L	17	155	12.7	0.48	1, 2, 10–12	38	108	7.0	0.15	3, 6, 7, 11, 12
<i>Capparis frondosa</i>	Capparaceae	Sh	21	334	2.8	0.61	1–3, 5	18	145	5.6	0.79	4–6
<i>Casearia arborea</i>	Flacourtiaceae	M	17	614	8.1	0.49	6–8, 11, 12	23	64518	8.9	0.92	8, 9
<i>Casearia sylvestris</i>	Flacourtiaceae	Sh	12	208	9.9	0.41	2, 8–12	–	–	–	–	–
<i>Cassipourea elliptica</i>	Rhizophoraceae	S	19	663	7.6	0.60	5–9	17	18271	9.7	0.91	9, 10
<i>Cavanillesia platanifolia</i>	Bombacaceae	L	–	–	–	–	–	11	19	4.6	0.99	4
<i>Cayaponia granatensis</i>	Cucurbitaceae	V	–	–	–	–	–	14	34	4.4	0.92	3, 4
<i>Cecropia insignis</i>	Cecropiaceae	L	18	891	3.2	0.61	1–5	100	51829	5.3	0.91	4, 5
<i>Ceiba pentandra</i>	Bombacaceae	L	–	–	–	–	–	25	84	3.3	0.98	2, 3
<i>Celtis iguanaea</i>	Ulmaceae	Li	–	–	–	–	–	57	348	10.1	0.52	9–11
<i>Ceratophyllum tetragonolobum</i>	Bignoniaceae	Li	26	78	4.8	0.82	3–5	34	422	5.9	0.79	5
<i>Chromolaena odorata</i>	Asteraceae	Sh	–	–	–	–	–	23	32	11.3	0.31	2, 4, 9
<i>Chrysophyllum argenteum</i>	Sapotaceae	L	–	–	–	–	–	18	32	2.7	0.89	2, 3
<i>Chrysophyllum cainito</i>	Sapotaceae	L	–	–	–	–	–	90	1226	2.9	0.96	2, 3

Appendix 2. Continued.

Species	Family	Life form	Flowering					Seeds				
			No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.	No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.
<i>Cinnamomum triplinerve</i>	Lauraceae	L	–	–	–	–	–	17	22	8.1	0.65	4, 5, 8, 9
<i>Cissus erosa</i>	Vitaceae	V	14	268	9.9	0.90	8–10	48	438	11.9	0.93	11, 12
<i>Clitoria javitensis</i>	Fabaceae	Li	11	171	2.0	0.78	1–3, 12	–	–	–	–	–
<i>Clusia flavida</i>	Clusiaceae	H	32	989	2.7	0.35	1–6, 12	156	53314	7.5	0.48	5, 6, 8, 9
<i>Coccoloba coronata</i>	Polygonaceae	S	–	–	–	–	–	18	36	1.2	0.80	1, 2, 10
<i>Coccoloba parimensis</i>	Polygonaceae	Li	37	149	5.7	0.90	5, 6	113	617	10.5	0.87	9–11
<i>Codonanthe crassifolia</i>	Gesneriaceae	E	21	140	6.5	0.41	4–9	24	254	8.6	0.24	5, 6, 10, 11
<i>Codonanthe uleana</i>	Gesneriaceae	E	16	72	6.5	0.40	4–6, 8, 9	17	296	6.7	0.47	4, 6, 7, 9
<i>Combretum decandrum</i>	Combretaceae	Li	27	165	4.1	0.95	3, 4	59	845	5.3	0.93	4, 5
<i>Combretum laxum</i>	Combretaceae	Li	11	82	11.6	0.30	3, 4, 10, 11	10	903	3.6	0.82	2–4
<i>Conarus turczaninowii</i>	Connaraceae	Li	–	–	–	–	–	12	17	7.5	0.83	6–8
<i>Cordia alliodora</i>	Boraginaceae	L	147	1597	3.4	0.95	2, 3	79	2821	4.9	0.97	4, 5
<i>Cordia bicolor</i>	Boraginaceae	M	51	962	3.3	0.89	2–4	118	3752	6.1	0.92	5, 6
<i>Cordia lasiocalyx</i>	Boraginaceae	S	62	1375	3.5	0.95	2, 3	127	1153	5.0	0.94	4, 5
<i>Coussapoa villosa</i>	Cecropiaceae	H	12	850	3.7	0.23	1–6, 8, 10	–	–	–	–	–
<i>Coussarea curvigemma</i>	Rubiaceae	S	17	232	6.7	0.94	6, 7	54	680	12.7	0.87	1, 11, 12
<i>Croton billbergianus</i>	Euphorbiaceae	S	–	–	–	–	–	12	112	9.1	0.89	7–9
<i>Cupania rufescens</i>	Sapindaceae	S	–	–	–	–	–	21	36	5.1	0.76	4, 5
<i>Cupania sylvatica</i>	Sapindaceae	S	–	–	–	–	–	14	15	5.6	0.79	4–6
<i>Cydista aequinoctialis</i>	Bignoniaceae	Li	76	812	6.5	0.74	5–8	97	606	3.7	0.77	2–4
<i>Davilla nitida</i>	Dilleniaceae	Li	39	254	2.4	0.82	1–3	87	533	4.3	0.95	3, 4
<i>Dendropanax arboreus</i>	Araliaceae	L	19	460	8.5	0.93	7, 8	147	4520	10.4	0.94	9, 10
<i>Desmopsis panamensis</i>	Annonaceae	S	21	58	1.8	0.43	2–4, 9–11	81	388	4.5	0.33	2–6, 10, 12
<i>Dipteryx oleifera</i>	Fabaceae	L	87	3273	7.5	0.91	6–8	50	614	2.0	0.89	1, 2
<i>Doliocarpus major</i>	Dilleniaceae	Li	61	524	7.1	0.83	6, 7	130	1551	10.2	0.85	9–11
<i>Doliocarpus multiflorus</i>	Dilleniaceae	Li	21	192	2.6	0.80	1–3	51	1516	4.7	0.76	3–5
<i>Doliocarpus olivaceus</i>	Dilleniaceae	Li	58	557	5.7	0.86	4–6	99	1099	10.2	0.91	9, 10
<i>Drypetes standleyi</i>	Euphorbiaceae	L	–	–	–	–	–	42	572	9.9	0.92	9, 10
<i>Entada monostachya</i>	Fabaceae	Li	46	1236	4.1	0.42	1–5, 9	10	39	10.9	0.57	8–12
<i>Epiphyllum phyllanthus</i>	Cactaceae	E	–	–	–	–	–	44	461	9.4	0.62	8–10
<i>Eugenia coloradoensis</i>	Myrtaceae	S	16	134	6.2	0.94	5, 6	29	270	10.0	0.83	8–10
<i>Eugenia nesiotica</i>	Myrtaceae	S	11	53	4.3	0.86	3, 4	–	–	–	–	–
<i>Eugenia oerstediana</i>	Myrtaceae	S	34	110	1.7	0.81	1, 2	160	1568	3.0	0.94	2, 3
<i>Faramaea occidentalis</i>	Rubiaceae	S	151	4035	6.0	0.90	5, 6	199	13906	11.8	0.83	10–12
<i>Garcinia intermedia</i>	Clusiaceae	L	–	–	–	–	–	21	71	5.4	0.90	4, 5
<i>Genipa americana</i>	Rubiaceae	L	–	–	–	–	–	21	2389	6.2	0.67	4–6, 8
<i>Guapira standleyana</i>	Nyctaginaceae	L	24	493	4.7	0.70	3–5	93	726	6.4	0.83	5–7
<i>Guarea grandifolia</i>	Meliaceae	L	–	–	–	–	–	33	529	3.1	0.89	2, 3
<i>Guarea guidonia</i>	Meliaceae	M	26	451	6.6	0.69	5–7, 10	117	769	3.4	0.88	2–4
<i>Guatteria dumetorum</i>	Annonaceae	L	36	2901	1.2	0.17	1–4, 9–12	129	878	3.4	0.67	1–4
<i>Guazuma ulmifolia</i>	Sterculiaceae	M	16	596	11.5	0.58	10, 11	–	–	–	–	–
<i>Guettarda foliacea</i>	Rubiaceae	S	–	–	–	–	–	11	74	11.8	0.94	11, 12

<i>Gustavia superba</i>	Lecythidaceae	S	24	1429	4.5	0.87	3–5	30	1013	6.3	0.90	5–7
<i>Hampea appendiculata</i>	Malvaceae	S	–	–	–	–	–	69	196	1.4	0.97	1
<i>Hasseltia floribunda</i>	Flacourtiaceae	S	32	498	4.6	0.74	3–5	102	3093	6.2	0.92	5, 6
<i>Heisteria acuminata</i>	Olacaceae	L	–	–	–	–	–	24	36	9.4	0.61	7, 8, 10, 11
<i>Heisteria concinna</i>	Olacaceae	M	40	591	12.8	0.60	1, 11, 12	101	721	3.8	0.87	2–4
<i>Hieronyma alchorneoides</i>	Euphorbiaceae	L	–	–	–	–	–	159	55936	– ¹	– ¹	1, 5, 6, 12
<i>Hippocratea volubilis</i>	Hippocrateaceae	L	62	1418	– ¹	– ¹	2–4, 7, 8, 10	65	1900	2.4	0.76	1–3, 12
<i>Hiraea faginea</i>	Malpighiaceae	Li	38	218	7.5	0.36	3–5, 8, 9, 11	44	941	5.6	0.51	3, 4, 6, 7
<i>Hiraea grandifolia</i>	Malpighiaceae	V	50	140	– ¹	– ¹	2, 4, 10–12	96	779	4.7	0.77	3–5
<i>Hiraea reclinata</i>	Malpighiaceae	Li	148	1445	3.8	0.71	2–5	164	2759	4.4	0.77	3–5
<i>Hiraea smilacina</i>	Malpighiaceae	Li	35	74	8.7	0.32	2–4, 8, 12	12	42	10.5	0.75	10
<i>Hirtella triandra</i>	Chrysobalanaceae	M	110	4793	4.4	0.39	1–5, 9	86	575	7.0	0.46	5–7, 10
<i>Hura crepitans</i>	Euphorbiaceae	L	23	3344	7.4	0.34	5–7, 10–12	12	29	12.2	0.39	1, 4, 9–11
<i>Hybanthus prunifolius</i>	Violaceae	Sh	111	1136	4.2	0.89	3–5	188	19196	4.9	0.92	4, 5
<i>Inga marginata</i>	Fabaceae	S	15	118	– ¹	– ¹	1, 2, 4, 5, 11, 12	107	516	2.2	0.30	1–3, 7, 12
<i>Jacaranda copaia</i>	Bignoniaceae	L	88	2089	3.9	0.93	3, 4	–	–	–	–	–
<i>Justicia graciliflora</i>	Acanthaceae	V	15	504	1.8	0.90	1, 2	–	–	–	–	–
<i>Lacmellea panamensis</i>	Apocynaceae	L	–	–	–	–	–	44	139	3.7	0.63	2–5, 12
<i>Laetia procera</i>	Flacourtiaceae	L	11	720	3.1	0.29	1–5, 10, 11	24	2727	5.1	0.66	3–6
<i>Laetia thamnia</i>	Flacourtiaceae	S	12	125	5.3	0.64	3–6	–	–	–	–	–
<i>Lindackeria laurina</i>	Flacourtiaceae	S	–	–	–	–	–	32	93	1.4	0.84	1, 12
<i>Lonchocarpus heptaphyllus</i>	Fabaceae	L	26	123	3.2	0.85	2, 3, 5	27	141	6.2	0.88	5, 6
<i>Luehea seemanii</i>	Tiliaceae	L	77	2246	2.3	0.92	1, 2	–	–	–	–	–
<i>Macfadyena unguis-cati</i>	Bignoniaceae	Li	50	243	4.5	0.68	3–5, 8	93	768	4.0	0.75	2–4
<i>Machaerium isadelphum</i>	Fabaceae	Li	13	114	3.5	0.88	2–4	26	480	5.8	0.87	4–6
<i>Maripa panamensis</i>	Convolvulaceae	Li	107	2167	3.8	0.90	2–4	108	734	6.9	0.87	6, 7
<i>Markea ulei</i>	Solanaceae	H	12	61	7.9	0.46	3, 6–9	–	–	–	–	–
<i>Martinella obovata</i>	Bignoniaceae	Li	–	–	–	–	–	18	56	2.0	0.46	2, 9, 10
<i>Mascagnia hiraea</i>	Malpighiaceae	Li	49	269	5.2	0.76	4–6	80	1653	5.8	0.88	4–6
<i>Mascagnia ovatifolia</i>	Malpighiaceae	Li	105	973	2.7	0.79	1–3	198	35056	3.9	0.88	3, 4
<i>Mendoncia gracilis</i>	Acanthaceae	V	35	966	8.3	0.73	6–9	83	618	11.3	0.82	10–12
<i>Mendoncia litoralis</i>	Acanthaceae	V	13	144	10.5	0.70	9–12	29	129	1.8	0.63	1–3, 12
<i>Mikania leiostachya</i>	Asteraceae	V	195	1362	3.9	0.96	3, 4	–	–	–	–	–
<i>Mosammona garwoodii</i>	Annonaceae	M	–	–	–	–	–	26	38	1.1	0.83	2, 11, 12
<i>Mouriri myrtilloides</i>	Melastomataceae	Sh	38	697	12.2	0.38	2, 3, 9–11	112	650	3.7	0.50	2, 3, 6–8
<i>Nectandra savannarum</i>	Lauraceae	S	–	–	–	–	–	10	31	4.4	0.97	4, 5
<i>Neea amplifolia</i>	Nyctaginaceae	S	–	–	–	–	–	21	30	10.4	0.67	2, 9, 10
<i>Ochroma pyramidale</i>	Bombacaceae	L	–	–	–	–	–	40	70	4.5	0.94	4, 5
<i>Ocotea cernua</i>	Lauraceae	M	–	–	–	–	–	28	42	4.3	0.56	3, 4, 9
<i>Ocotea oblonga</i>	Lauraceae	L	–	–	–	–	–	29	80	7.3	0.37	4, 8, 9
<i>Ocotea whitei</i>	Lauraceae	L	13	487	3.9	0.90	3, 4	17	125	6.8	0.71	5–8
<i>Oenocarpus mapora</i>	Arecaceae	M	95	3699	2.1	0.59	1–4, 12	119	1254	7.5	0.70	6–9
<i>Oncidium stipitatum</i>	Orchidaceae	E	28	40	3.2	0.95	2, 3	–	–	–	–	–
<i>Oryctanthus alveolatus</i>	Loranthaceae	P	25	142	8.8	0.09	1, 3, 6–8, 10, 11	56	206	10.0	0.24	3, 5–8, 10, 11
<i>Ouratea lucens</i>	Ochnaceae	Sh	14	291	2.0	0.76	1–3, 12	17	38	3.3	0.59	2–4, 8

Appendix 2. Continued.

Species	Family	Life form	Flowering					Seeds				
			No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.	No. of traps	No. of obs.	Mean month	Mean vector	Months inc. 75% of obs.
<i>Palicourea guianensis</i>	Rubiaceae	Sh	–	–	–	–	–	79	1098	10.5	0.90	9–11
<i>Paragonia pyramidata</i>	Bignoniaceae	Li	50	429	3.8	0.79	2–4	66	844	8.6	0.75	7–9
<i>Paullinia baileyi</i>	Sapindaceae	Li	22	107	5.8	0.56	4, 5, 8–10	38	102	11.3	0.64	9, 10, 12
<i>Paullinia fibrigera</i>	Sapindaceae	Li	17	163	10.9	0.97	10, 11	70	323	12.4	0.88	10, 12
<i>Paullinia fuscescens</i>	Sapindaceae	Li	52	283	1.8	0.88	1, 2	61	778	4.0	0.95	3, 4
<i>Paullinia rugosa</i>	Sapindaceae	Li	24	266	9.0	0.87	8, 9	40	346	10.5	0.93	9, 10
<i>Paullinia turbacensis</i>	Sapindaceae	Li	28	208	1.4	0.87	1, 12	74	159	3.5	0.83	3, 4
<i>Peperomia macrostachya</i>	Piperaceae	E	11	17	5.4	0.46	2–6, 8	–	–	–	–	–
<i>Petrea volubilis</i>	Verbenaceae	Li	70	458	4.7	0.85	3–5	39	181	5.5	0.92	4–6
<i>Phryganocydia corymbosa</i>	Bignoniaceae	Li	39	303	8.8	0.57	6, 7, 9–11	56	255	10.0	0.22	4, 5, 8–10
<i>Phthirusa pyrifolia</i>	Loranthaceae	P	–	–	–	–	–	10	15	7.4	0.46	1, 5, 7, 10
<i>Picramnia latifolia</i>	Picramniaceae	S	–	–	–	–	–	14	213	5.2	0.98	4, 5
<i>Pithecoctenium crucigerum</i>	Bignoniaceae	Li	11	132	6.2	0.93	5, 6	93	836	1.6	0.40	3, 4, 10, 11
<i>Platymiscium pinnatum</i>	Fabaceae	L	46	351	5.0	0.92	4, 5	46	383	3.1	0.59	1–4
<i>Platypodium elegans</i>	Fabaceae	L	105	850	4.9	0.95	4, 5	55	567	3.4	0.67	2–5
<i>Poulsenia armata</i>	Moraceae	L	24	639	– ¹	– ¹	1, 5, 6, 8–12	38	347	6.5	0.48	2, 4–7, 10
<i>Pouteria reticulata</i>	Sapotaceae	L	37	606	5.0	0.80	3–5	78	489	8.7	0.88	7–9
<i>Prestonia obovata</i>	Apocynaceae	Li	–	–	–	–	–	21	41	4.1	0.82	3, 4
<i>Prestonia portobellensis</i>	Apocynaceae	Li	–	–	–	–	–	20	27	3.4	0.60	1–5
<i>Prionostemma aspera</i>	Hippocrateaceae	Li	77	1709	2.9	0.79	2–4	63	364	3.5	0.68	2–5
<i>Prioria copaifera</i>	Fabaceae	L	64	3784	– ¹	– ¹	2–4, 9–11	14	259	4.6	0.85	3–5
<i>Protium panamense</i>	Burseraceae	L	22	37	5.3	0.72	4–7, 10	–	–	–	–	–
<i>Protium tenuifolium</i>	Burseraceae	L	29	440	5.4	0.89	4–6	86	639	8.5	0.91	7–9
<i>Pseudobombax septenatum</i>	Bombacaceae	L	–	–	–	–	–	20	105	4.5	0.98	3, 4
<i>Psiguria warscewiczii</i>	Cucurbitaceae	V	–	–	–	–	–	21	119	10.1	0.29	6, 10, 11
<i>Psychotria hoffmannseggiana</i>	Rubiaceae	Sh	–	–	–	–	–	30	104	12.2	0.73	1, 11, 12
<i>Psychotria horizontalis</i>	Rubiaceae	Sh	19	146	5.6	0.90	5, 6	140	2401	11.1	0.89	10–12
<i>Pterocarpus rohrii</i>	Fabaceae	L	14	59	4.9	0.71	1, 5, 6	13	137	10.5	0.92	10, 11
<i>Quararibea asterolepis</i>	Bombacaceae	L	97	4248	6.9	0.70	5–7	182	21814	9.5	0.86	8–10
<i>Quassia amara</i>	Simaroubaceae	S	17	41	12.2	0.50	1, 7, 12	–	–	–	–	–
<i>Randia armata</i>	Rubiaceae	S	12	178	5.6	0.90	5, 6	149	4601	7.9	0.79	6–8
<i>Rhynchosia pyramidalis</i>	Fabaceae	Li	33	271	2.6	0.90	1–3	25	42	5.1	0.80	4, 5
<i>Rinorea sylvatica</i>	Violaceae	Sh	16	138	3.6	0.79	1–4	18	169	4.9	0.64	2, 4, 6
<i>Sapium glandulosum</i>	Euphorbiaceae	M	–	–	–	–	–	34	233	9.0	0.91	8, 9
<i>Schefflera morototoni</i>	Araliaceae	M	–	–	–	–	–	–	–	–	–	–
<i>Serjania atrolineata</i>	Sapindaceae	Li	22	55	1.4	0.83	1, 12	15	33	4.6	0.97	4, 5
<i>Serjania circumvallata</i>	Sapindaceae	Li	73	668	1.4	0.84	1, 12	144	3622	4.7	0.90	3–5
<i>Serjania decapleuria</i>	Sapindaceae	Li	10	152	1.5	0.84	1, 12	12	382	3.6	0.92	3, 4
<i>Serjania mexicana</i>	Sapindaceae	Li	42	421	3.2	0.78	1, 3, 4, 12	103	5473	4.9	0.93	4, 5
<i>Serjania pluvialiflorens</i>	Sapindaceae	Li	15	136	11.1	0.50	1, 8–10, 12	35	578	2.5	0.49	1–4, 11, 12
<i>Simarouba amara</i>	Simaroubaceae	S	43	951	3.2	0.94	2, 3	80	1092	5.1	0.94	4, 5
<i>Sloanea terniflora</i>	Elaeocarpaceae	L	11	569	8.4	0.29	3, 4, 6–10	22	455	1.9	0.28	1–3, 8, 9, 11
<i>Smilax mollis</i>	Smilacaceae	V	–	–	–	–	–	24	47	11.3	0.74	9–12
<i>Solanum hayesii</i>	Solanaceae	Sh	–	–	–	–	–	16	11559	6.9	0.80	5–7

<i>Sorocea affinis</i>	Moraceae	Sh	20	178	8.4	0.73	7–9	106	636	11.4	0.93	10, 11
<i>Souroubea sympetala</i>	Marcgraviaceae	H	15	1237	2.7	0.57	1–4, 12	26	1360	4.9	0.50	1, 3–6
<i>Spondias mombin</i>	Anacardiaceae	L	28	293	4.9	0.95	4, 5	49	349	9.6	0.97	9
<i>Spondias radlkoferi</i>	Anacardiaceae	L	24	653	5.2	0.63	3–5, 9	57	413	10.9	0.88	10, 11
<i>Stigmaphyllon lindenianum</i>	Malpighiaceae	Li	11	79	3.5	0.63	1–4	23	189	5.8	0.54	3–7
<i>Stizophyllum riparium</i>	Bignoniaceae	Li	–	–	–	–	–	25	38	3.2	0.43	1–4, 6, 12
<i>Struthanthus orbicularis</i>	Loranthaceae	P	15	114	4.9	0.81	4–6	36	118	8.4	0.35	3, 6–9, 11
<i>Strychnos panamensis</i>	Loganiaceae	Li	–	–	–	–	–	22	281	5.5	0.36	3–6, 9
<i>Stylogyne turbacensis</i>	Myrsinaceae	S	–	–	–	–	–	18	22	4.8	0.56	3–5, 8
<i>Swartzia simplex</i> var. <i>grandiflora</i>	Fabaceae	S	13	23	6.5	0.84	5–7	–	–	–	–	–
<i>Swartzia simplex</i> var. <i>continentalis</i>	Fabaceae	S	28	194	5.8	0.87	5, 6	14	19	2.3	0.82	1–3
<i>Symphonia globulifera</i>	Clusiaceae	L	12	443	6.1	0.47	3–8	–	–	–	–	–
<i>Tabebuia guayacan</i>	Bignoniaceae	L	37	438	4.3	0.88	3–5	80	2688	5.8	0.93	5, 6
<i>Tabebuia rosea</i>	Bignoniaceae	L	24	226	3.5	0.92	2–4	162	3128	4.7	0.95	4, 5
<i>Tabernaemontana arborea</i>	Apocynaceae	L	63	3708	4.1	0.70	2–5	43	1208	4.7	0.57	1, 4–6
<i>Tachigali versicolor</i>	Fabaceae	L	–	–	–	–	–	11	22	3.9	0.82	2–4
<i>Terminalia oblonga</i>	Combretaceae	S	–	–	–	–	–	52	573	4.1	0.81	3–5
<i>Tetracera hydrophila</i>	Dilleniaceae	Li	28	¹	¹	0.11	3, 5–8, 10–12	67	1163	9.1	0.22	3, 4, 7, 8, 10, 11
<i>Tetracera portobellensis</i>	Dilleniaceae	Li	–	–	–	–	–	19	30	3.8	0.95	3, 4
<i>Tetracera volubilis</i>	Dilleniaceae	Li	12	17	7.4	0.23	1, 7	–	–	–	–	–
<i>Tetragastris panamensis</i>	Burseraceae	L	54	2612	8.1	0.45	1, 6–10	120	3077	3.7	0.60	1–5
<i>Tetrapteryx discolor</i>	Malpighiaceae	Li	27	217	2.4	0.88	1, 2	38	481	4.8	0.86	3–5
<i>Tetrapteryx goudotiana</i>	Malpighiaceae	Li	14	131	8.2	0.57	5, 7–9	10	336	1.6	0.74	1–3, 12
<i>Thinouia myriantha</i>	Sapindaceae	Li	84	1108	2.3	0.94	1, 2	137	10802	4.1	0.92	3, 4
<i>Topobea parasitica</i>	Melastomataceae	H	18	492	6.7	0.71	5–8	–	–	–	–	–
<i>Trattinnickia aspera</i>	Burseraceae	L	–	–	–	–	–	94	327	2.6	0.67	1–4
<i>Trema micrantha</i>	Ulmaceae	M	19	419	5.6	0.80	4–6	11	2704	9.1	0.84	8–10
<i>Trichilia pallida</i>	Meliaceae	M	–	–	–	–	–	32	576	9.6	0.75	8–11
<i>Trichilia tuberculata</i>	Meliaceae	L	132	4759	5.9	0.58	3–7	199	35876	9.5	0.91	8–10
<i>Trichospermum galeottii</i>	Tiliaceae	M	–	–	–	–	–	12	244	2.6	0.72	2, 3, 12
<i>Triplaris cumingiana</i>	Polygonaceae	M	49	1066	3.4	0.96	2, 3	48	1822	4.5	0.90	3–5
<i>Tynanthus croatianus</i>	Bignoniaceae	Li	37	248	8.1	0.75	7–9	105	12075	3.2	0.89	2–4
<i>Uncaria tomentosa</i>	Rubiaceae	Li	22	158	4.3	0.82	3, 4	–	–	–	–	–
<i>Unonopsis pittieri</i>	Annonaceae	M	–	–	–	–	–	17	240	3.0	0.63	1–4
<i>Virola multiflora</i>	Myristicaceae	M	–	–	–	–	–	15	259	2.6	0.42	1–5, 12
<i>Virola sebifera</i>	Myristicaceae	L	64	2428	5.3	0.51	3–7	119	1170	12.2	0.73	1, 10–12
<i>Virola surinamensis</i>	Myristicaceae	L	42	1278	12.8	0.66	1, 2, 10–12	108	719	6.6	0.58	4–8
<i>Vochysia ferruginea</i>	Vochysiaceae	L	14	486	5.5	0.89	4–6	–	–	–	–	–
<i>Xylopia macrantha</i>	Annonaceae	M	–	–	–	–	–	12	95	5.3	0.67	3, 5, 9
<i>Zanthoxylum ekmanii</i>	Rutaceae	L	40	715	10.1	0.95	9, 10	90	455	3.1	0.77	2–4
<i>Zanthoxylum panamense</i>	Rutaceae	M	31	181	6.9	0.62	5, 6, 10	82	4135	10.5	0.86	10, 11
<i>Zuelania guidonia</i>	Flacourtiaceae	L	–	–	–	–	–	11	430	8.1	0.73	7–9

¹Mean month and vector cannot be calculated because the species exhibits significant bimodality.