Phenological patterns and reproductive success of *Ceiba pentandra* (Bombacaceae) in tropical dry and wet forests of Costa Rica

Patrones fenológicos y éxito reproductivo de *Ceiba pentandra* (Bombacaceae) en el bosque tropical seco y húmedo de Costa Rica

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ABSTRACT

We studied the phenological patterns and the reproductive success of 103 *Ceiba pentandra* trees, located in the tropical dry and wet forests of the Pacific coast of Costa Rica. To determine the phenological patterns of this species we recorded leaf fall, flower and fruit production of marked trees every two-weeks from December through March over three years (2001, 2002 and 2003). We also recorded the flowering and fruiting frequencies for two more years (2000 and 2004). Our data suggest that phenological patterns of *C. pentandra* trees behave as irregular cycles rather than cycles fixed at supra-annual intervals, and the forest type in which the trees are located does not have a decisive effect on either the probability or the frequency of the reproductive cycles. The absence of a pattern of negative autocorrelations in qualitative reproductive success (e.g., no reproduction, only flowers and fruits) among successive years suggests that the flowering or fruiting cycles of this species do not correspond to a simple model of resource limitation. Our results show that there is no relationship between the reproductive success and the periodicity of the reproductive cycles in this species.

Key words: *Ceiba pentandra*, Costa Rica, reproductive success, supra-annual phenology.

RESUMEN

Estudiamos los patrones fenológicos y el éxito reproductivo de 103 árboles de *Ceiba pentandra*, localizados en el bosque tropical seco y en el bosque tropical húmedo de la costa del Pacífico de Costa Rica. Para determinar los patrones fenológicos se anotó la caída de hojas y la producción de flores y frutos cada dos semanas desde diciembre hasta marzo para todos los árboles marcados por un periodo de tres años (2001, 2002 y 2003). También se tomaron datos de la frecuencia de floración y fructificación para dos años más (2000 y 2004). Nuestros datos sugieren que los patrones fenológicos de árboles de *C. pentandra* se comportan como ciclos irregulares más que como ciclos fijos de intervalos supraanuales y el tipo de bosque en el cual los árboles se ubican no está teniendo un efecto decisivo ni en la probabilidad ni en la frecuencia de los ciclos reproductivos. La ausencia de patrones de autocorrelación negativa en el éxito reproductivo (no reproducción, solamente floración y fructificación) en años sucesivos nos sugiere que los ciclos de floración y fructificación para esta especie no corresponden a un modelo simple de limitación de recursos. Nuestros resultados muestran que no existe una relación entre el éxito reproductivo y la periodicidad de los ciclos reproductivos para esta especie.

Palabras clave: *Ceiba pentandra*, Costa Rica, éxito reproductivo, fenología supra-anual.

INTRODUCTION

Supra-annual reproductive phenology in plants occurs when individual phenological episodes recur cyclically on a time interval that surpasses a single year (Newstrom et al. 1994). Frankie et al. (1974) reported this behavior for approximately 10 % of tropical trees species of the dry and wet tropical forest in the lowlands of Costa Rica. Other authors have suggested that this pattern occurs in nearly 50 % of tropical trees species in forests of southeast of Asia (Sakai et al. 1999, 2006).

Light, humidity, temperature, photoperiod and irradiance have been proposed as cues that trigger reproductive phenological events in tropical plant species (Opler et al. 1976, Borchert 1983, van Schaik 1986, Asthon et al. 1988, Tutin & Fernández 1993, Newstrom et al. 1994, Wright & van Schaik 1994, Sun et al. 1996). In addition to abiotic factors, models based on storage and expense of resources for reproduction have been proposed to explain the fluctuating patterns of flowering intensity in plants (Isagi et al. 1997, Rees et al. 2002, Crone et al. 2003). These models predict the occurrence of populational synchronization and patterns of negative autocorrelation in reproductive individuals in successive years; that is, if a plant reproduces in a given year it will be less likely to reproduce in the following year. Such patterns are characteristic of many species with supra-annual cycles and/or mast seeding (Kelly & Sork 2002, Koenig et al. 2003).

Supra-annual flowering phenology has also been associated with mast seeding reproductive patterns (Herrera et al. 1998, Sakai et al. 1999). Plants that exhibit mast seeding have reproductive episodes with high or low seed production and the variation in reproductive episodes is large (Kelly & Sork 2002, Buonaccorsi et al. 2003). When supra-annual flowering cycles of individual plants are highly synchronized, extreme mast seeding events are likely to occur. This has been shown for Dipterocarp species of the southeast of Asia (Sakai et al. 1999, 2006). However, species with individuals exhibiting supra-annual phenology but with low flowering synchrony at the population level tend to show less variability in fruit production between years (Buonaccorsi et al. 2003).

Supra-annual phenology and mast seeding represent the extremes of a reproductive pattern present in many species of plants, in which the intensity of flowering and fruiting varies greatly between reproductive episodes (Frankie et al. 1974, Baker 1983, Kelly & Sork 2002, Lobo et al. 2003). Indeed, some studies propose that these variations are the result of adaptive strategies that avoid seed predation (i.e., predator satiation hypothesis), attract pollinators or enhance outcrossing (Janzen 1971, Horvitz & Schemke 1995, Kelly & Sork 2002).

Ceiba pentandra is a pan-tropical canopy tree of tropical dry and wet forests. Native populations occur in tropical America and West Africa and it was probably introduced by man in South-East Asia (Baker 1983). In the Neotropics, the reproductive phenology of this species has been described as irregular, with variable phenophases and cycles with multiyear time spans, and with great variation in reproductive intensity between populations and years (Frankie et al. 1974, Newstrom et al. 1994, Gribel et al. 1999, Lobo et al. 2003). Indeed, variation in reproductive intensity has been observed for this species not only at temporary scale (e.g., within populations and among years), but also to spatial scale (e.g., between different populations within the same year) (Lobo et al. 2003).

The flowering and fruiting activity of *C. pentandra* are limited to the dry season in Neotropical forests (Frankie et al. 1974, Gribel et al. 1999). Along the Pacific coast of Central America, trees located at different latitudes (from 19º30' N in Chamela to 8º26' N in the Osa Peninsula) flower simultaneously in January (Lobo et al. 2003). The frequency and intensity of the reproductive episodes, however, exhibit notable geographical and temporal variation (Frankie et al.1974, Baker 1983, Newstrom et al. 1994, Gribel et al. 1999, Lobo et al. 2003). Nevertheless, no studies have evaluated the tendency of tropical trees to exhibit negative autocorrelations of reproduction in successive years. Furthermore, the relationship between fruit-set and reproductive synchronization has not been determined at the population level for supra-annual species. The relationship between leaf and flowering phenology needs clarification, and it is unknown if both behave independently in species with supra-annual phenological patterns.

The main goal of this study was to provide data on the reproductive biology and phenological patterns of *Ceiba pentandra* populations located in the tropical dry and wet forests of the Pacific coast of Costa Rica. Specifically, our objectives were to (1) evaluate the relationship between leaf fall and supra-annual reproductive events, (2) determine tendency for negative autocorrelation on the reproduction over consecutive years, and (3) evaluate the effect of forest type (e.g., dry versus

wet forest) on the frequency of the reproductive cycles and the reproductive success (e.g., no reproduction, only flowers and fruits).

MATERIAL AND METHODS

Study species

Ceiba pentandra (Bombacaceae) is distributed from Mexico to the south of the Amazonian basin and in the paleotropic throughout western Africa (Hartshorn 1983). *Ceiba pentandra* has hermaphroditic and chiropterophilic flowers with five stamens around a protruding style, pink petals and nocturnal anthesis (Cascante 1997). The fruits are elliptic, and seeds are surrounded by a pale yellow silk cotton, used for wind dispersion. This species is an emergent deciduous tree that may reach heights of more than 60 m, and in Neotropical populations pollination process has been attributed mainly to phyllostomid bats (Gribel et al. 1999, Lobo et al. 2005).

Study sites

We performed our study in two tropical forests of Costa Rica with different precipitation patterns. The first site was the tropical dry forest located in the north Pacific coast of Costa Rica in the province of Guanacaste (10º45' N, 84º30' W). Average annual rainfall on this area is 1500 mm and the dry season extends from December through April (Coen 1983, Gómez & Herrera 1985). Average temperature during the dry season ranges from 32.5 to 21.9 ºC. Here we recorded trees located along 88 km on the Pan-American Road from Esparza (460 m of altitude) to Bagaces (90 m of altitude). We will refer to this site as dry forest.

The second site was the tropical wet forest located in the South Pacific coast of Costa Rica. The dry season in this site extends from December to April but it is not as intense as the tropical dry forest (Coen 1983, Gómez & Herrera 1985). The average annual rainfall on this area is 3800 mm and the average temperature during the dry season ranges from 31.8 to 21.7 ºC (Gómez & Herrera 1985). Here we identified four populations: two populations were situated along the Pan-American road in the Osa Peninsula. The first population was located along 38 km on the road between Boruca (9º0' N, 83º28' W, 452 m of altitude) and Chacarita (8º46' N, 83º14' W, 278 m of altitude) and the second population was located along 19 km on the road between La Palma (8º39' N, 83º29' W, 1 m of altitude) and Puerto Jimenez (8º31' N, 83º20' W, 9 m of altitude). The other two populations were located one within the Golfo Dulce Forestry Reserve (8º36' N, 83º33' W, 200 m of altitude) and the other one near Sirena Biological Station within the Corcovado National Park (8º27' N, 83º42' W, 45 m of altitude). We will refer to these sites as wet forest.

Selection of trees

We selected *C. pentandra* reproductive adults with a diameter-at-breast-height greater than 1 m. We classified each tree as either isolated or occurring in continuous forests. Trees were considered isolated when they were surrounded by agricultural fields or pastures and occurred at more than 1 km from the nearest forest fragment. Trees were considered to be in continuous forest when they were surrounded by at least 50 ha of natural forest. In the dry forest of Guanacaste all the studied trees (n = 35) were isolated and this sample represent the total of reproductive trees along the 88 km of road that we sampled. In the wet forest of the South Pacific Coast, we identified two populations of isolated trees (Boruca-Chacarita: n = 14; La Palma-Puerto Jimenez: n = 30) and two more populations consisted of trees in continuous forest (Golfo Dulce Forestry Reserve: n = 8; and Sirena Biological Station: n = 16). For these sites, the two isolated populations represent most of the reproductive trees along the two roads sampled and the other two populations on continuous forests represent near 50 % of the reproductive population.

Phenological observations

In order to determine the sequence of phenological phases of trees, we recorded the phenology of marked trees every two-weeks from November to March for three years (2001, 2002 and 2003), starting on 1 November each year. We began observations in November with the objective to capture the beginning of

phenological changes that occurred during December. Trees were observed with binoculars and phenology of leaves, flowers and fruits were determined based on the percentage of cover of the crown as suggested by Fournier (1974). This method allows a quantitative estimation of phenological phases using a scale with values between 0-4. Each value correspond to the following phenological behavior: (0) absence of the phenological characteristic, (1) presence of the phenological characteristic with a range from 1-25 %, (2) presence of the phenological characteristic with a range from 26-50 %, (3) presence of the phenological characteristic with a range from 51–75 %, (4) presence of the phenological characteristic with a range from 76–100 % (Fournier 1974).

For each year and forest type, trees were classified into three categories of reproductive success. Reproductive success was measured in terms of flowers that converted into fruits. The three categories of reproductive success were: (1) no reproduction (no blossoms or flowers observed), (2) partial or complete flower crown cover, but no fruiting), and (3) at least one branch with fruits observed. In addition, reproductive success observations of 15 isolated trees in dry forest in year 2000 and 36 isolated trees in wet forest in year 2004 and were included in the analysis in order to allow the comparison of the reproductive success in a period of four years in each forest type. For these two years (2000 and 2004), we performed the same methodology mentioned previously for phenological observations for years 2001, 2002 and 2003.

Data analysis

We performed a heterogeneity Chi-square test to compare phenological patterns among years and forest types (dry or wet forest). Using this analysis we were able to compare the percentages of trees with leaf fall, flowering or fruiting, every two-week from December-March. To perform this analysis we considered that a tree was flowering when it had 10 % or more of the crown covered with flowers. The same condition was used to determinate when a tree was fruiting.

To study the variation in the probability of flowering and fruiting events, we compared the number of trees flowering or fruiting over four

years (2000, 2001, 2002 and 2003 for dry forest and 2001, 2002, 2003 and 2004 for wet forest). We used a Logistic Regression Analysis to determine the effect of year, forest type (dry or wet forest) and isolation condition (isolated or continuous forest), on flowering and fruiting probability. The isolation condition term was only used for the analysis of the wet forest because in the dry forest we only sampled isolated trees. The same analysis was also used to estimate the effect of previous reproductive event on the probability of flowering and fruiting in a given year. Forest type, isolation condition and reproductive success of the previous year were used as independent variables and the proportion of flowering trees and trees that set fruits were used as response variables. The effect of forest type and year was determined only for years where data from dry and wet forest were obtained (2001-2003). The isolation condition effect was determined only for tree populations located in wet forest, where observations on the reproductive frequency of trees in continuous and isolated forest were available.

To test the influence of previous reproduction on flowering or fruiting probability, we used all trees (n = 68 trees) that we recorded for the three years analyzed, independently of site and isolated condition. We used the flowering or fruiting event in years 2001 and 2002 as independent variables, and the flowering or fruiting event in year 2003 as the response variable. In year 2003 almost 40 % of the trees flowered and set fruit in both forest types. Significance of effects was tested by the likelihood ratio statistic between the model with and without the effect. This statistic follows a X^2 distribution with degrees of freedom equal to the number of parameters tested (Stokes et al. 2000). In cases were the effects were significant, the sign of the effect was determined by inspection of the regression coefficient or the associated odds ratio (Stokes et al. 2000).

<div align="center">RESULTS</div>

Phenological patterns

Ceiba pentandra trees lost their leaves between December and January, during the dry season in both dry and wet forest (Fig. 1 and 2). For

both forest types, leaf fall activity reached its peak in the beginning of January. By the beginning of March, most trees had flushed large quantities of new leaves and by April, all trees were in full leaf (Fig. 1 and 2). However, trees that did not reproduce in a specific year generally produced new leaves few days after leaf fall event, remaining a small period of time in deciduous condition. This behavior is the reason to observe a significant percentage of trees (> 10 %) within populations with leaves in any moment throughout the dry season (Fig. 1 and 2).

For this species, flowering was also restricted to the dry season in both dry and wet forests. In the dry forest for the three years analyzed, trees started to display flowers by the beginning of January and flowering activity peaked at the end of January or beginning of February (Fig. 1). In the wet forest, for years 2001 and 2002 flowering activity started in the end of December or beginning of January. However in 2003, trees bloomed prematurely and flowers were present on some trees in early December (Fig. 2). Flowering peaks occurred in 2001 and 2002 during January, but in 2003 this process took place during the last two-weeks of December and the first two-weeks of January. Indeed, for 2003 during the last two-weeks of December 78 % of the trees were flowering, and this percentage was significantly greater compared to the 40 % of flowering trees for the same date in year 2001 (X^2 = 11.2, df = 1, P < 0.01) and the 11 % of flowering trees for the same date in year 2002 (X^2 = 54.9, df = 1, P < 0.01) (Fig. 2).

In regards to fruiting, in dry forest this activity started at the beginning of January and increased gradually until it reached a peak at the end of February for year 2001; however for years 2002 and 2003 fruiting began at the end of January and increased until reached a peak in March (Fig. 1). For wet forest in years 2001 and 2003 fruiting began in the last two-weeks of December and increased gradually until it reached a peak in February for year 2001 and in March for year 2003. For year 2002 this activity was delayed until the last days of January and peaked in March (Fig. 2).

Reproductive success

The percentage of individuals that flowered and fruited varied depending on forest type and year (Fig. 3). The lowest reproductive success was observed in 2004 for wet forest, when only 10 % of the trees flowered and 2.8 % of the trees matured fruits. In other words, for this year only 27 % of the flowers have been converted into fruits (Fig. 3). In contrast, the greatest reproductive success was recorded in 2000 for dry forest and in 2003 for wet forest when approximately 75 % of trees flowered and 70-45 % of trees matured fruits (Fig. 3).

Logistic regression analysis of 2001–2003 data showed that *C. pentandra* significantly differed in flowering frequency among years (X^2 = 74.11, df = 2, P < 0.01) and forest types (X^2 = 8.09, df = 1, P < 0.01), as a result of the higher flowering frequency recorded in wet forest in year 2003. However, the interaction term among year and forest type was also significant (X^2 = 18.8, df = 2, P < 0.01), indicating that the higher frequency of flowering in wet forest for year 2003 was not observed in other years. This analysis also demonstrated that the probability of flowering for *C. pentandra,* independent of forest type, was greatest in year 2003 compared to years 2001 and 2002, but there were no differences between years 2001 and 2002 (Odds Ratio 2001/2003 = 0.423, 95 % CI = 0.11-0.44, Odds Ratio 2002/2003 = 0.20, 95 % CI = 0.11-0.37, Odds Ratio 2001/2002 = 1.02, 95 % CI = 0.53-1.95).

No differences were observed in fruiting frequency between trees in dry and wet forest (X^2 = 3.56, df = 1, P > 0.05). The probability to set fruit, independently of forest type, was greatest for year 2003 compared to years 2001 and 2002, but there were no differences between years 2001 and 2002 (Odds Ratio 2001/2003 = 0.46, 95 % CI = 0.23-0.91 Odds Ratio 2002/2003 = 0.44, 95 % CI = 0.22-0.74, Odds Ratio 2001/2002 = 1.06, 95 % CI = 0.51-2.18).

No differences were observed in flowering (X^2 = 0.05, df =1, P > 0.05) and fruiting frequencies (X^2 = 6.41, df = 1, P > 0.01), between isolated trees and trees in continuous forest (Fig. 4). Both populations showed high reproductive success in years of high global reproduction (i.e., 2003) and viceversa (Fig. 4).

Reproduction data recorded during years 2001-2003 for dry and wet forests shown that fruit set measured as the proportion of fruiting trees/flowering trees, was not affected by year
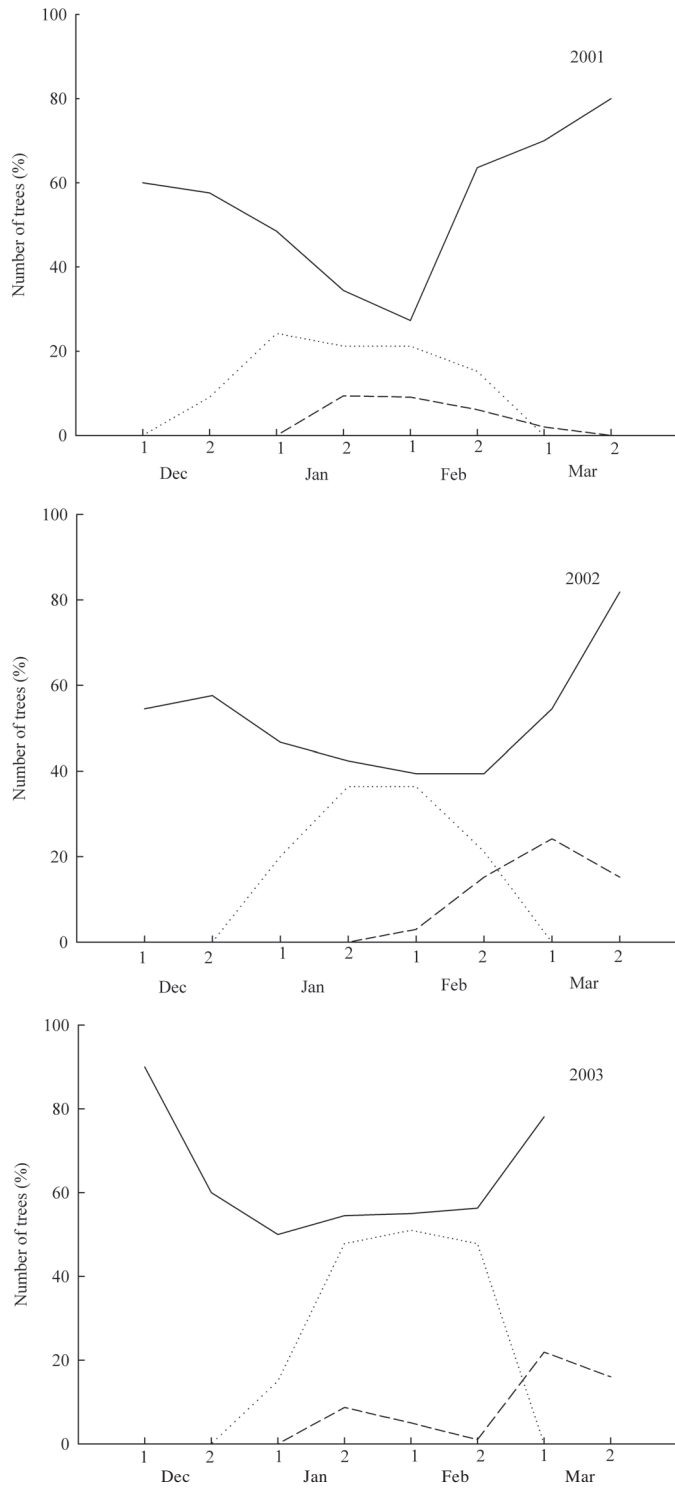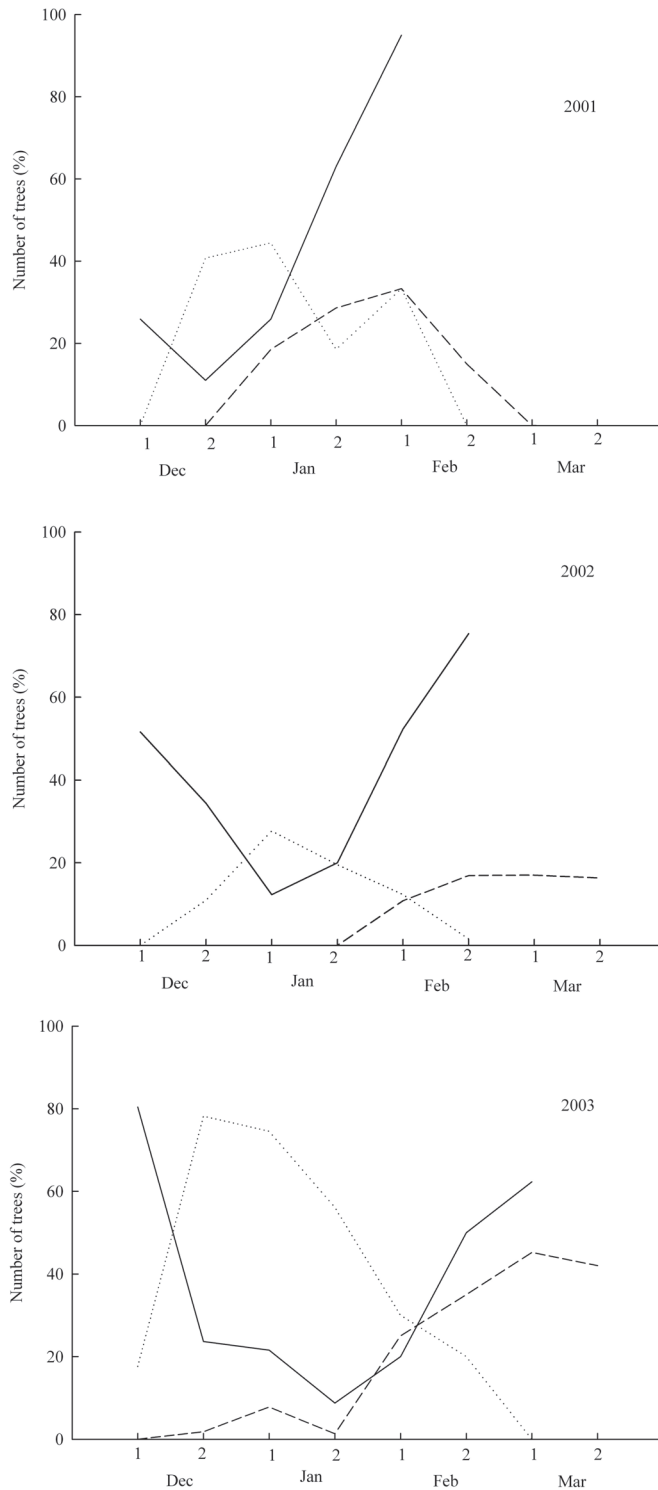
Fig. 1: Percentage of the population of *Ceiba pentandra* trees with leaves (————), flowers (·········) and fruits (- - - - -) in tropical dry forests of Guanacaste. Data were recorded every two-weeks (one and two for each month) during dry season over three years.

Porcentaje de la población de árboles de *Ceiba pentandra* con hojas (————), flores (·········) y frutos (- - - - -) en el bosque tropical seco de Guanacaste. Los datos fueron tomados cada quincena (uno y dos para cada mes) durante la estación seca por tres años.

Fig. 2: Percentage of the population of *Ceiba pentandra* trees with leaves (———), flowers (·········) and fruits (- - - - -) in tropical wet forests of the Osa Peninsula. Data were recorded every two-weeks (one and two for each month) during dry season over three years.

Porcentaje de la población de árboles de *Ceiba pentandra* con hojas (———), flores (·········) y frutos (- - - - -) en el bosque tropical húmedo de la Península de Osa. Los datos fueron tomados cada quincena (uno y dos para cada mes) durante la estación seca por tres años.
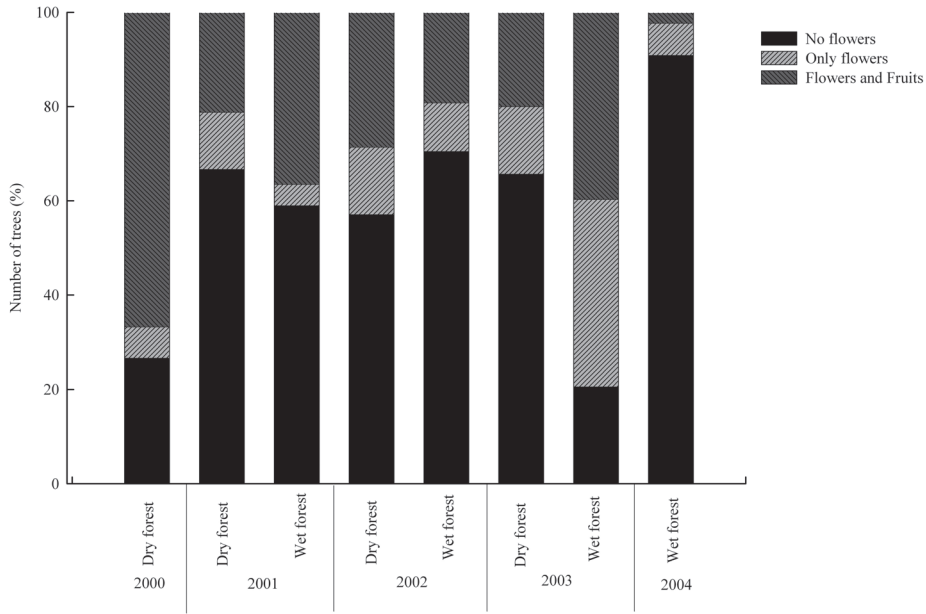
Fig. 3: Percentage of *Ceiba pentandra* trees flowering and fruiting in tropical dry and wet forests of Costa Rica between 2000 and 2004. Dry forest sample size 2000-2003: (15, 31, 33, 31 trees). Wet forest sample size 2001-2004: (37, 68, 68, 44 trees).

Porcentaje de árboles de *Ceiba pentandra* florecidos y fructificados en bosque tropical seco y húmedo de Costa Rica entre 2001 y 2004. Tamaño de muestra bosque seco 2000-2003: (15, 31, 33, 31 árboles). Tamaño de muestra bosque húmedo 2001-2004: (37, 68, 68, 44 árboles).
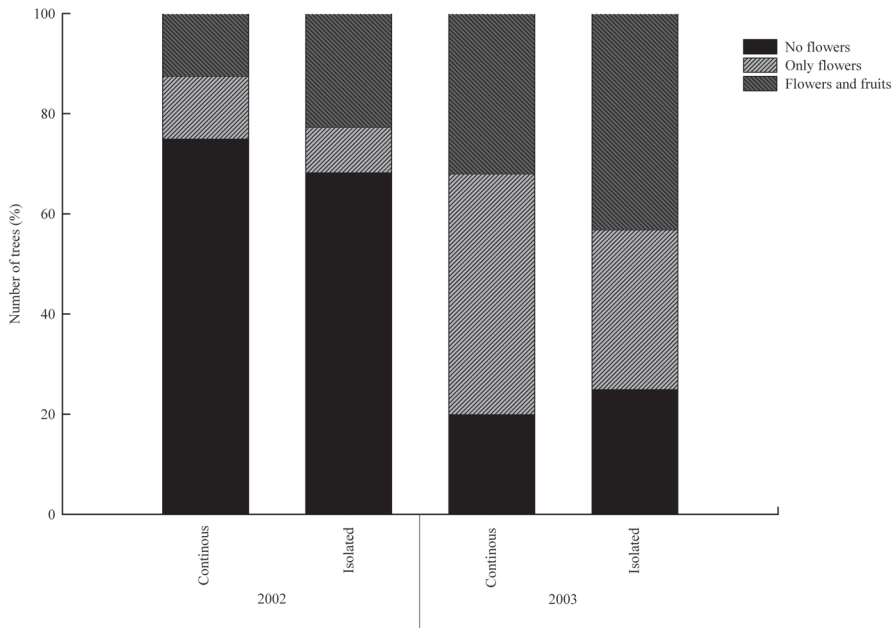

Fig. 4: Percentage of *Ceiba pentandra* trees flowering and fruiting in continuous (n = 24 trees) and isolated (n = 44 trees) tropical wet forest of Costa Rica.

Porcentaje de árboles de *Ceiba pentandra* florecidos y fructificados en bosque tropical húmedo continuo (n = 24 árboles) y aislado (n = 44 árboles) de Costa Rica.

($X^2 = 4.0$, df = 4, P > 0.05), nor by forest type ($X^2 = 1.18$, df = 1, P > 0.05). The greatest flowering frequency occurred in year 2003, but it did not translate into a great fruiting event. The percentage of fruiting trees/flowering trees varied between 58-73 % during years 2001-2003. However, trees in isolated condition showed higher fruiting/flowering ratio (ratio ≈ 0.75) than trees in continuous forest (ratio ≈ 0.37, $X^2 = 11.85$, df = 1, P < 0.01), when trees in both conditions were compared for wet forest (Fig. 4).

Reproduction periodicity

Irregularity in flowering and fruiting cycles was observed for the two forest types. Indeed, the majority of trees flowered and fruited one or two times in the four years analyzed (Table 1). Phenological patterns of fruits production, similar to the results of flowers production on the previous section, were irregular and did not follow supra-annual cycles of a fixed number of years, neither at population or individual levels. The lack of supra-annual cycles is supported by the fact that the probability of a given tree flowering/fruiting in one of the most successful years in terms of reproduction (i.e., 2003) was not strongly influenced by the reproductive event in previous years. Logistic Regression Analysis demonstrated that the probability of flowering in 2003 was independent of the flowering success of the trees in 2001 ($X^2 = 0.47$, df = 1, P > 0.05), the fruiting success of the trees in 2001 ($X^2 = 0.39$, df = 1, P > 0.05) and the fruiting success of the

trees in 2002 ($X^2 = 0.62$, df = 1, P > 0.05). Flowering probability in the 2003 was influenced by the flowering success in the previous year (2002) ($X^2 = 5.99$, df = 1, 0.01 < P < 0.05). Trees that not flowered the previous year had a lower probability of flowering in 2003 (β≤ = -28.27, SE = 1.39).

Effect of previous reproduction on the fruiting probability in 2003 follows the same pattern as the flowering event. Probability of fruiting in 2003 was independent of fruiting success in 2001 ($X^2 = 2.77$, df = 1, P > 0.05), fruiting success in 2002 ($X^2 = 2.21$, df = 1, P > 0.05) and flowering success in 2001 ($X^2 = 0.60$, df = 1, P > 0.05). A significant effect of the flowering event in the 2002 ($X^2 = 4.43$, df = 1, 0.01 > P > 0.05) was detected on the fruiting success in 2003, probably as a consequence of the correlation of flowering success between the two years.

DISCUSSION

Our study shows that the leaf fall, flowering and fruiting components of the phenological cycles of *C. pentandra* were limited to the dry season (December-April) in Costa Rica, in both dry and wet forests. Previous studies documented the same phenological patterns for *C. pentandra* in Brazil, Mexico, Panama and Costa Rica (Frankie et al. 1974, Baker 1983, Murawski & Hamrick 1992, Gribbel et al. 1999, Lobo et al. 2003).

We observed that phenological cycles of *C. pentandra* are irregular among individuals

TABLE 1

Flowering and fruiting frequency of 68 trees of *Ceiba pentandra* in tropical dry and wet forests of Costa Rica between 2001 and 2003

Frecuencias de floración y fructificación de 68 árboles de *Ceiba pentandra* en el bosque tropical seco y húmedo de Costa Rica entre 2001 y 2003

Number of annual flowering episodes	Number of trees		Number of annual fruiting episodes	Number of trees	
	Dry forest	Wet forest		Dry forest	Wet forest
0	11	3	0	14	7
1	12	15	1	18	15
2	8	11	2	4	8
3	3	5	3	0	2
Total	34	34	Total	36	32

within populations, in accordance to what has described previously for this species (Frankie et al. 1974, Baker 1983). We defined the term irregular as a behavior in which the phenological cycles do not occur in a fixed time interval at the individual level, although at the population level the flowering process is limited to few weeks of the year. From our sample of trees, some individuals reproduced every year during the dry season, while many others showed a variable duration between each flowering and fruiting episode. Most *C. pentandra* trees lost and replaced their leaves every year. The flowering and fruiting activities, however, were not as regular as leaf replacement activity. Although complete leaf abscission is a necessary but not sufficient condition for the start of flowering activity. The loss of leaves does not necessarily predict the production of flowers on *C. pentanda* trees; and like other tropical trees, flowering activity for this species might be determined by the presence of complementary abiotic signals that trigger the maturation of flower buds (Frankie et al. 1974, Opler et al. 1980, Borchert 1994, Chapman et al. 1999, Sakai et al. 2006).

From our data we suggested that most of the variation observed at the time intervals of leaf abscission, flowering and fruiting process may be attributed to differences among years rather than between forest types. The onset of vegetative and reproductive activity was similar among *C. pentandra* populations in both the dry and wet forests. The time intervals of these phenological events were strikingly similar between forest types in spite of great difference between them in the beginning date, duration and intensity of the dry season. Indeed, during the years of this study, the average monthly rainfall during the dry season was of 0.7 mm for the whole season in the dry forest of Costa Rica and 182.9 mm in the wet forests.

The phenological patterns revealed by this study are in accordance with observations of Lobo et al. (2003). They suggested that for *C. pentandra*, the environmental signs that determine the onset of leaf-loss, flowering and fruiting are not predictable from humidity in the soil and local precipitation, as have been proposed for some tropical dry forest tree species (Borchert 1994). A possible explanation for this disassociation between

changes in soil humidity and the triggering of some phenophase may be explained by the combination of a deep central root system with the ability to store water inside the tree trunks (Borchert 1994, Machado & Tyree 1994).

In regarding the reproductive periodicity, although the time interval of flowering of *C. pentandra* occurred at the beginning of the dry season across years, and the probability of a tree of flowering was also irregular across years, the phenological reproductive pattern observed in this species showed a strict categorical expression (i.e., either reproduce or not in a given year). For example, non-reproductive individuals do not even produce flower meristems. These individuals commonly lose their leaves in December or at the beginning of January and, may produce new leaves immediately after defoliation process or may remain defoliated without any evidence of reproductive activity until the producction of new leaves of the subsequent season.

Based on these observations, we conclude that is not possible to predict the phenological behavior of a tree from one year to the next. Indeed, we observed that groups of trees subject to very similar environmental conditions of humidity and light (i.e., trees located in the same forest type and isolation condition), often showed phenological behaviors completely different. This observation suggests that the phenological patterns of *C. pentandra* may be regulated by endogenous or internal cycles, which vary among individuals within the same population of trees. Our observations do not suggest any particular controlling mechanism for individual reproductive periodicity.

In addition, our study shows the absence of negative autocorrelation between individual reproductive events between years, because the probability of reproduction was not determined by the reproduction of the previous year. The only weak association observed was found between the probability of flowering in a given year with the probability of flowering the previous year. However, this correlation was a positive, contrary to the expectation of a model based on accumulation and investment of resources for reproduction (lsagi et al. 1997, Rees et al. 2002). A positive correlation of the probability of flowering between two successive years can be explained by variation in the

reproductive frequency between trees. Models of mast seeding can also explain this pattern if there is a high variance between individuals in the storage and acquisition of resources or the threshold for triggering reproduction (Crone et al. 2005). It has been suggested that the reproductive strategies of supra-annual phenology and mast-seeding are the result of adaptations selected to increase the reproductive success by increasing pollination rate during years of massive simultaneous flowering activity. However, we found that in years with high flowering frequency, there was not a proportional increase in the probability to set fruits. For both forest types, years with exceptionally high flowering activity did not translated into years with greater probability of set fruits, because there were massive abortions of flower buds and developing fruits. Flowers and immature fruits may selectively abort due to aspects related to pollination, seed production or maternal effects (Stephenson 1981).

In conclusion, our study suggested that phenological patterns of *C. pentandra* behave as irregular cycles rather than cycles fixed at supra-annual intervals, and that the forest type in which trees are located (i.e., dry or wet forest) does not have a decisive effect on the probability nor the frequency of the reproductive cycles. Finally, it is important to coordinate long-term studies to further the understanding of phenological patterns of tropical trees and the cues that trigger them.

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