

REPRODUCTIVE PHENOLOGY OF THE MAIN TREE SPECIES IN THE RORAIMA SAVANNA, BRAZILIAN AMAZON

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Abstract. The reproductive phenological patterns were investigated in the three most abundant tree species in the Roraima open savanna: *Curatella americana* L.f. (Dilleniaceae), *Byrsonima crassifolia* (L.) Kunth, and *B. coccolobifolia* Kunth (Malpighiaceae). A total of 112 trees were marked for study over a period of 24 months (2001–2003), and the existence of climatic synchrony and duration of phenological phases that characterize the reproductive patterns of each population were investigated. The results indicate (i) in *C. americana* and *B. crassifolia* reproductive phenological events were strongly associated with low amounts of rainfall, but climatic synchrony was not clearly pronounced in *B. coccolobifolia*, (ii) each species demonstrated its own distinct phenophase duration and population synchrony, and (iii) the phenological pattern for the three species can be defined as *intermediate* (between the beginning and end of the dry season), with all species using zoochory as the principal means of seed dispersal. We conclude that for all three species, the majority of phenological events occur during the dry season peak, which corresponds to the lowest amount of cloud cover and the highest amount of insolation across most of the savanna in Roraima. The phenological patterns and the reproductive cycles of the three species studied are similar to those observed in other savanna regions of Brazilian Amazonia and Venezuela.

Keywords: Amazonia, reproductive phenology, *Curatella*, *Byrsonima*, climatic synchrony.

INTRODUCTION

Phenological events are the best plant reproduction and vegetative space-time descriptors in terrestrial ecosystems, generally occurring in direct synchrony with the occurrence of climatic events (Rathcke & Lacey 1985, Newstrom *et al.* 1994, Morellato *et al.* 2000). An investigation of these phenological processes is necessary to understand periods of reproduction, growth, and establishment of plant species. Knowledge of these processes is especially important in tropical savannas and grasslands because plant

species in these ecosystems are strongly affected by climatic seasonality, hydric stress, and high fire frequency (Monasterio & Sarmiento 1976, Felfili *et al.* 1999, Ramírez & Briceño 2011). These factors can affect the production of fruit and flowers, with profound consequences for the availability of trophic resources for vertebrates and invertebrates (Sanaiotti & Magnusson 1995, Ramírez 2002). Studies on the reproductive phenological patterns in savannas can elucidate how climatic seasonality drives reproductive patterns of plant populations and communities (Miranda 1995, Silvério & Lenza 2010). Characterization of these reproductive events will improve man-

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agement strategies and conservation of these open vegetation environments.

In the case of the Brazilian Amazon, most studies have focused on plant reproductive patterns in forest environments and species (e.g. Ferreira & Parolin (2007) investigated how water level fluctuation affects the phenology of floodplain forests and Brando *et al.* (2006) studied the effect of partial throughfall exclusion on the phenology of a forest species). However, few studies have been conducted in Amazonian savannas and grasslands, despite the fact that these open systems represent about 5% (~ 200 000 km²) of the entire Amazon (Santos *et al.* 2007). Although savanna enclaves are scattered throughout the Amazonian region, the largest is located in the state of Roraima (commonly referred to as *lavrado*). The *lavrado* is the largest continuous, non-forest ecosystem in the Amazonian biome (~ 43 000 km²), located in the border region of Brazil, Venezuela, and Guyana (Barbosa *et al.* 2007, Barbosa & Campos 2011).

Previous research on the composition and structure of the tree-shrub community in Roraima indicates low plant diversity and large geographical floristic distance relative to conspecifics in the Central Brazilian savannas (Ratter *et al.* 2003). Most of the open savanna habitats in Roraima are dominated by three tree species: *Curatella americana* L.f. (Dilleniaceae), *Byrsonima crassifolia* (L.) Kunth, and *B. coccolobifolia* Kunth (Malpighiaceae) (Miranda *et al.* 2002, Barbosa *et al.* 2005). On average, these species represent ~ 60-70% of all individual trees or ~ 80% of the tree above-ground biomass found in these open environments (Barbosa & Fearnside 2005). These tree species can be considered key species given their abundance and critical role in ecological succession and maintenance of the Roraima savanna (Mourão Jr. *et al.* 2010). Characterizing the phenological patterns of these key species will provide insight into their principal growth and reproductive strategies, as well as the supply of trophic resources to local fauna (Reys *et al.* 2005).

The aim of this research was to study the reproductive phenological patterns of the three main tree species in the Roraima savanna. We investigated whether reproductive events are synchronized with climate, and quantified the duration of the phenological phases of each studied population. We asked the following questions: (i) Are the reproductive events of these three species synchronized with regional rainfall dynamics (climatic synchrony)?

(ii) Does phenophase duration differ between species? This is the first study of phenological patterns in plant populations of open savanna areas in Roraima.

MATERIAL AND METHODS

Study Areas. This study was carried out in two open savanna sites near the capital of Roraima state, Boa Vista: (a) Monte Cristo Experimental Station (Embrapa Roraima), located 25 km northwest of Boa Vista (2°56'47"N, 60°43'02"W), and (b) Morada Nova Farm, in the vicinity of the Caraná Stream, 10 km west of Boa Vista (2°50'13"N, 60°44'42"W). In the Köppen classification system (Köppen 1936), the regional climate is defined as tropical dry (Aw) with an extended dry season during winter. Average annual rainfall is 1614 mm, with a dry season peak occurring between December and March and a rainy season between May and August (Barbosa 1997). The average monthly temperature remains constant throughout the entire year (27.8 ± 0.6°C), varying by no more than 5°C between the maximum and minimum monthly temperatures. The period of the year with the highest amount of daylight is between September and February, while the cloudiest period (overcast sky) is between March and August (Fig. 1).

Both sites have a flat relief and an altitude of ~100 m; parkland savanna is the typical physiognomy of the two areas. Both regions are situated in an Ultisol/Oxisol mosaic covered by a herbaceous strata dominated by various species of Poaceae (e.g. *Trachypogon* spp. and *Andropogon* spp.) and Cyperaceae (e.g. *Bulbostylis* spp. and *Eleocharis* spp.). The tree layer is typically dominated by *C. americana*, *B. crassifolia*, and *B. coccolobifolia*; all of them very common in open savanna regions. The three species are pollinated by bees (Ramírez 2004). *Curatella americana* is pollinated by *Apis mellifera* L. (Hymenoptera, Apidae). Flowers of the two species of *Byrsonima* spp. are mostly visited by solitary bees of *Centris* spp., *Epicharis* spp., and *Xylocopa* spp. (Centridini). *Curatella americana* produces a biloculate fruit with two seeds covered by white arils, while the fruits of both *Byrsonima* spp. are fleshy. The seeds of all three species are primarily dispersed by birds (zoochory), although a small number of seeds is dispersed by gravity (barichory) (Mourão Jr. *et al.* 2010). Leaf periodicity of *B. coccolobifolia* is brevi-deciduous (Benezar & Pessoni 2006) while *C. americana* and *B. crassifolia* are evergreen (Monasterio & Sarmiento 1976).

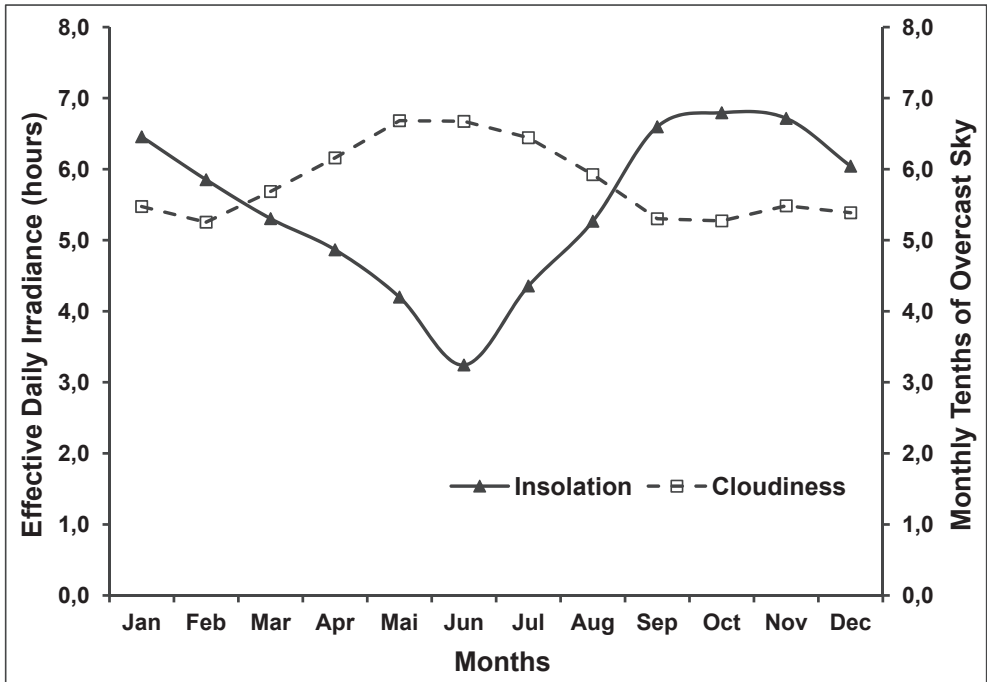


FIG. 1. Number of hours of effective daily irradiance (insolation) and mean monthly measure of overcast sky (cloudiness), measured in the city of Boa Vista, Roraima (Source: INMET-Brazil, National Institute of Meteorology).

Sampling methods. A linear transect of 250 m, starting at the geographical center of each study area and extending northward, was marked. All individuals of the three study species encountered up to a maximum distance of 2 m on either side of the central transect line were sampled. We only included individuals whose base diameter (Db), measured at 2 cm from the ground or from trunk protrusions, was greater than 2 cm. Based on previous observations we assumed that individuals with $Db < 2$ cm would not be able to fully reproduce (youngest), taking the base diameter as a rough chronological indicator. In total, 112 individuals were sampled in the two study areas (Monte Cristo; Morada Nova): *C. americana* (50; 7), *B. crassifolia* (4; 33), *B. coccolobifolia* (1; 17).

The activity index method defined by Bencke & Morelato (2002) was used to characterize the presence or absence of particular phenophases over a given period of time. This index is qualitative on an individual scale and quantitative on a population scale. The observed phenophases were (i) release of the flower bud (BF), (ii) presence of flowers during

anthesis (FL), and (iii) presence of fruit, independent of the maturity stage (FR). All of the observations were qualitative, noting presence or absence in each observed individual. The study was conducted over a period of 24 months (December 6, 2001 to December 5, 2003). Shorter intervals (15 days) were established during periods of higher concentrations of flowering and fruiting, while the longer intervals (> 15 days) were adopted during the peak rainy season.

Data analysis. The different phenophases were checked for seasonality (climatic synchrony) using the daily rainfall data for the city of Boa Vista as the climatic indicator. Discrete time-series data for each of the phenological responses were constructed using the Julian day calendar (later converted into a monthly calendar). We used a Durbin-Watson test for randomness (d) (Diggle 1991) to verify if the time series and repeated measurements during the period of time in question had a certain degree of autocorrelation (p), given the presence of seasonality. In cases where seasonality was detected, the degree and

direction of the association between phenological events and rainfall (total amount of rainfall in the seven days prior to the event) was determined by a Spearman's rank correlation (r_s).

To determine the duration of each of the reproductive phenophases, an individual synchrony measurement was created (x_i) (Eq. 1) for each of the evaluated species, aiming to represent the behavior of the population of the series sampled during the assessment cycle (Augspurger 1983, Almeida-Neto & Lewinsohn 2004).

$$x_i = \frac{1}{[f_i(n-1)]} \sum_{j=1}^n e_{izj} \quad (\text{Eq. 1})$$

Where: x_i is the individual synchrony coefficient; f_i is the number of duration periods of the i individual phenophase; e_{izj} is the number of periods in which the i and j individuals show the phenological event together; and n is the number of individuals found in the sample.

A Goodness of Fit test ($\chi^2_{0.05}$) was carried out to determine if the phenophase durations (BF, FR, FR) of the three populations were proportionally equal (1:1:1) in relation to each other. The general reproductive phenological pattern of each species was defined by means of the temporal distribution of the events observed in the field, according to the method

specified by Bulhão & Figueiredo (2002) and Figueiredo (2008). The phenological pattern of the three species was therefore defined in the following manner: (i) emergence of the event in relation to the dry period – *late* (final), *early* (initial), *intermediate* (between the beginning and end of the dry season); (ii) the duration of each of the events, (iii) population synchrony, and (iv) seed dispersal syndrome. We also classified the species by their reproductive cycles according to Newstrom *et al.* (1994): (i) *annual* – a single cycle per year and (ii) *sub-annual* – two reproductive cycles per year.

RESULTS

Climatic synchrony. The highest frequency of reproductive phenophases of the three species was observed during the season with low rainfall (dry season) (Fig. 2). *Curatella americana* and *B. crassifolia* showed significant, positive auto-correlation ($\alpha=0.05$), denoted by the Durbin-Watson statistic for all of the evaluated reproductive phenophases (Table 1). All phenophases of these two species had seasonality (strong climatic synchrony). *Byrsonima coccolobifolia* had significant positive auto-correlation for the flowering and fruiting processes, but the Durbin-Watson statistic was not conclusive in relation to flower budding.

TABLE 1. Statistical tests: Durbin-Watson values (d), auto-correlation (p) and Spearman's correlation (r_s) of the phenological events evaluated in savanna areas of Roraima (December 2001 - December 2003), where (*) = significantly positive auto-correlation ($\alpha=0.05$; $n=31$; $k=1$), nc = non-conclusive, (**) = Spearman's correlation highly significant and ns = non-significant.

Species	Phenophases	Durbin-Watson (d)	Auto-correlation coefficient (p)	Spearman (r_s)	t	P
<i>C. americana</i>	Flower Bud	0.725	0.637 (*)	-0.559	-3.631	0.001 (**)
	Flowering	0.875	0.562 (*)	-0.560	-3.641	0.001 (**)
	Fruiting	0.657	0.672 (*)	-0.553	-3.574	0.001 (**)
<i>B. crassifolia</i>	Flower Bud	0.880	0.560 (*)	-0.478	-2.928	0.006 (**)
	Flowering	0.543	0.728 (*)	-0.559	-3.628	0.001 (**)
	Fruiting	0.415	0.792 (*)	-0.468	-2.851	0.008 (**)
<i>B. coccolobifolia</i>	Flower Bud	1.356	0.322 nc	-0.298	-1.682	> 0.10 ns
	Flowering	1.319	0.340 (*)	-0.261	-1.456	> 0.10 ns
	Fruiting	0.685	0.658 (*)	-0.286	-1.610	> 0.10 ns

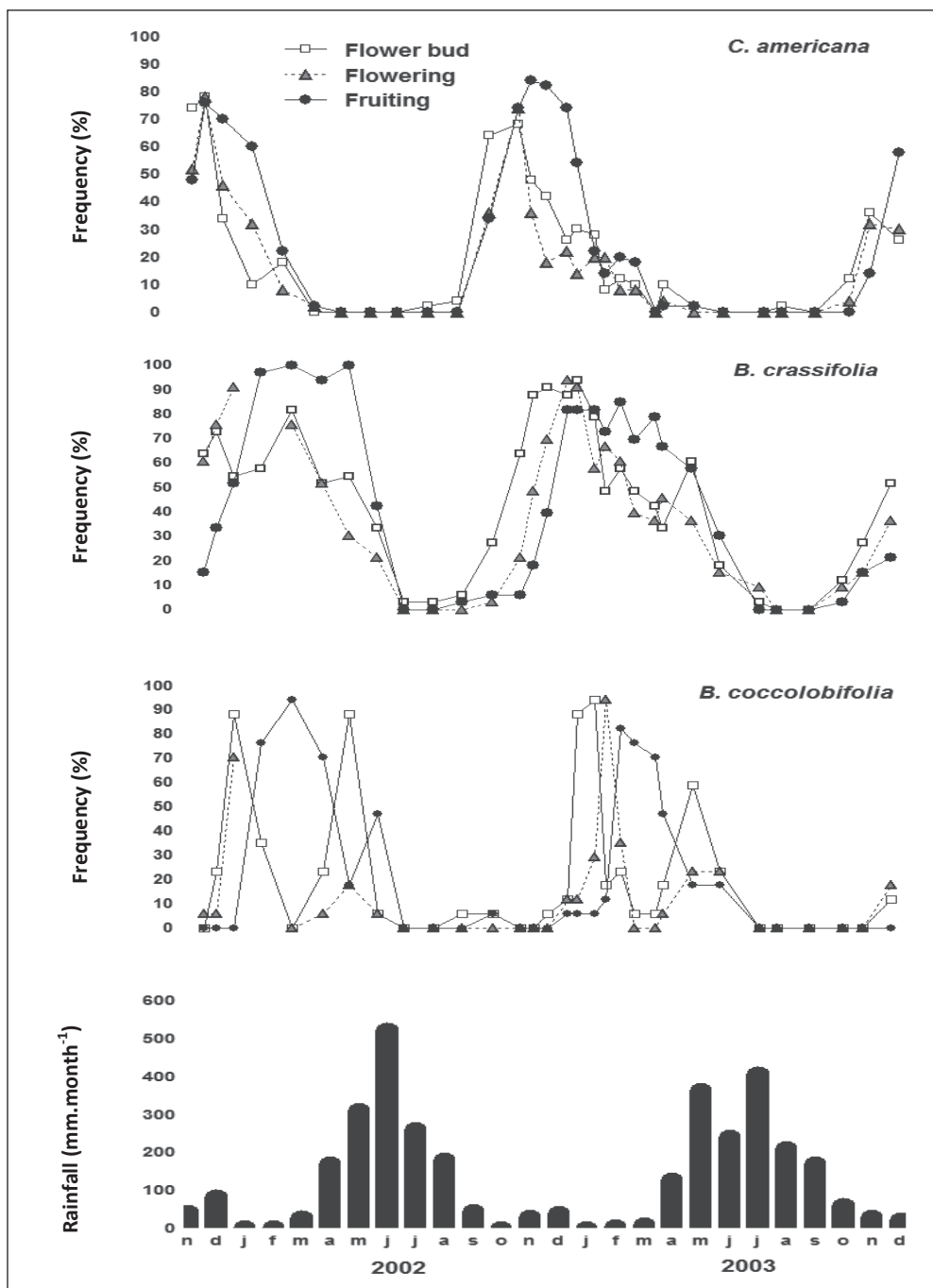


FIG. 2. Frequency (%) of individuals in the various reproductive phenophases, and mean monthly precipitation, in savanna areas of Roraima (December 2001 - December 2003) (Rainfall data source: INMET-Brazil, National Institute of Meteorology).

The Spearman's correlation between the phenophases and the amount of rainfall was negative; lower amounts of rainfall were associated with higher presence of the event (Table 1). However, only the reproductive phenophases of *C. americana* and *B. crassifolia* showed significant levels of association ($r_{S, 0.05(2), 31}; P < 0.001$). The *B. coccolobifolia* phenophases were negatively associated, but were not statistically influenced, reflected in the low significance of the Durbin-Watson statistic.

Duration of the phenophases. The three species had different phenological amplitudes (Fig. 3). *Curatella americana* had reproductive phases distributed between October and March – the driest period of the year. The duration of the reproductive phenophases of this species varied between 43 and 61 days, with population synchrony of 43-59%. The flowering spectrum of *B. crassifolia* was rather more widespread; a period established between September and June (entire dry season and the beginning of the rainy season). All *B. crassifolia* phenophases

lasted approximately 80 days, with population synchrony between 64 and 71%. *Byrsonima coccolobifolia* was the species with the lowest phenological amplitude (December to June), representing a small, secondary peak observed at the beginning of the rainy season. The population synchrony of this species was ~60% for all phenophases. The duration of all *B. coccolobifolia* phenophases (BF = 46; FL = 35; FR = 50 days) was statistically lower in comparison with *B. crassifolia* ($\chi^2_{0.05;2} = 5.991; 0.025 < P < 0.01$), but was non-significant in relation to *C. americana*.

Phenological patterns. Most reproductive phenological events of the three study species were associated with the dry season and, therefore, all species can be described by an *intermediate* pattern, with zoochory as the main seed-dispersal syndrome (Table 2). The frequency of the reproductive cycles of all species was regular, with *C. americana* and *B. crassifolia* representing annual cycles, and *B. coccolobifolia* a sub-annual cycle.

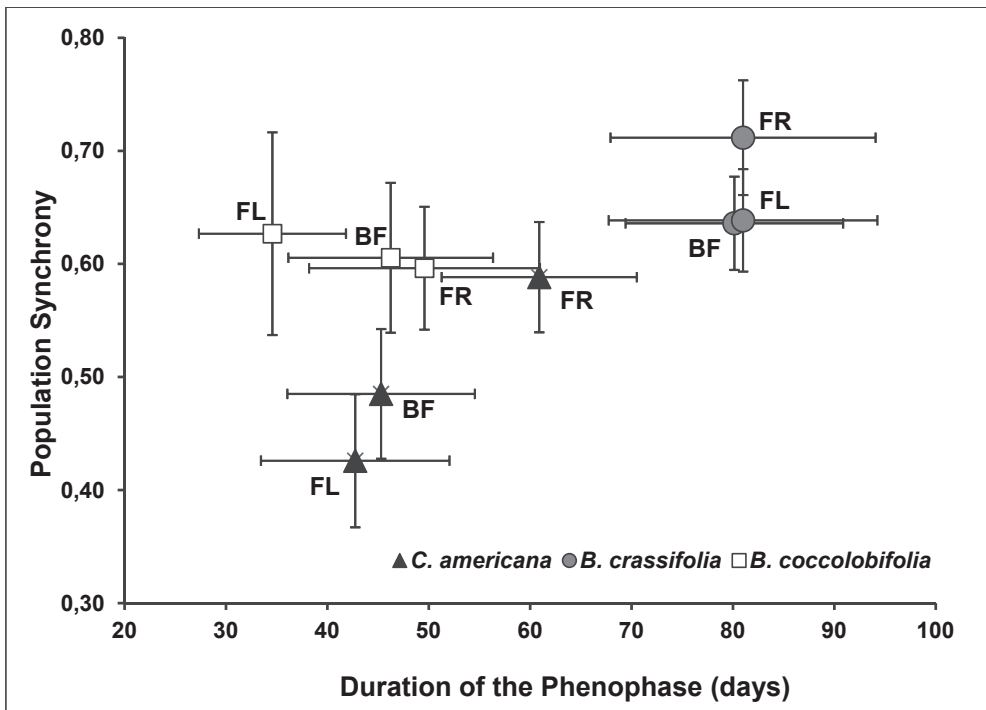


FIG. 3. Population synchrony and duration of the phenophases observed in savanna areas of Roraima (December 2001 - December 2003), where BF = flower bud, FL = flowering, FR = fruiting. Duration = days±SE, Synchrony = Freq%±SE (standard error).

TABLE 2. Reproductive phenological pattern of the three main tree species sampled in savanna areas of Roraima (December 2001 - December 2003), where \pm SE (standard error).

Species	Phenophases	Phenological Pattern (1)	Cycle / Frequency	Leaf periodicity	Dispersal Syndrome (2)	Duration (days \pm SE)	Synchrony (Freq% \pm SE)
<i>C. americana</i>	Flower Bud					45 \pm 9	0.49 \pm 0.06
	Flowering	Intermediate	Annual (Regular)	Evergreen	Zoochory	43 \pm 9	0.43 \pm 0.06
	Fruiting					61 \pm 10	0.59 \pm 0.05
<i>B. crassifolia</i>	Flower Bud					80 \pm 11	0.64 \pm 0.04
	Flowering	Intermediate	Annual (Regular)	Evergreen	Zoochory	81 \pm 13	0.64 \pm 0.05
	Fruiting					81 \pm 13	0.71 \pm 0.05
<i>B. coccolobifolia</i>	Flower Bud					46 \pm 10	0.61 \pm 0.07
	Flowering	Intermediate	Sub-annual (Regular)	Brevi-deciduous	Zoochory	35 \pm 7	0.63 \pm 0.09
	Fruiting					50 \pm 11	0.60 \pm 0.05

(1) Most events were observed in the dry season, although *B. coccolobifolia* and *B. crassifolia* have, respectively, a secondary flowering peak and the end of reproductive events at the beginning of the rainy season.

(2) All species show a certain amount of barichorous seed dispersal.

DISCUSSION

Most reproductive phenophases of *C. americana*, *B. crassifolia*, and *B. coccolobifolia* in the Roraima savanna were associated with the regional dry season (December-March). The majority of the tree species in the savanna of Alter do Chão (state of Pará, Brazil) also showed high concentrations of reproductive events during the dry season (Miranda 1995). The pattern observed in the Roraima savanna also matches that found in the Venezuelan Llanos for the flowering/fruitleting of *C. americana* and *B. crassifolia* (Monasterio & Sarmiento 1976, Sarmiento *et al.* 1985). The Llanos are situated relatively close to the savanna areas in Roraima (~850 km) and share similar climatic conditions, including a peak dry season between December and March. On the other hand, we did not find a strong climatic synchrony in *B. coccolobifolia*. This species is brevi-deciduous, having a small secondary flowering peak at the beginning of the rainy season, which may explain the lack of synchrony.

The association of reproductive events with the dry season has been shown in other tree species of dry tropical environments, and appears to be a survival strategy in a strongly seasonal climate, using the wettest periods to develop vegetative structures (Singh & Kushwaha 2005). This strategy allows for

fruit maturity and seed dispersal during the first rains, which may provide greater chances of germination and seedling establishment due to higher water availability in the soil and without the threat of fire (Williams *et al.* 1999). On the other hand, such strong relationships have also been observed in the Central Amazonian floodplain forests, where the reproductive cycle of tree species is strongly related to regular, long-term flooding (Schöngart *et al.* 2002, Parolin *et al.* 2010). In this case, the physiological consequences of the long-term flooding for tree species is the same as the dry season in the savannas. Both events lead to limited water availability for the roots due to droughts (savanna) or anoxic conditions (floodplains).

This general synchrony pattern was suggested by Janzen (1967) as a strategy employed by tropical trees to maximize the probability of successful pollination and dispersal. In addition, the ability of a plant species to coordinate reproductive events with changing abiotic conditions, such as the availability of light and the presence/absence of fire, is likely an evolutionary adaptation in environments with high climate seasonality. Thus the timing and frequency of the reproductive events in the savanna species studied may be similar to that of tropical forest trees, whereby biotic, climatic, and edaphic factors drive the flowering process (Borchert 1983, 1994; Schaik *et al.* 1993).

The synchrony pattern detected in this study, when compared with other types of study carried out in the savannas of the Brazilian Central Plateau (Cerrado Biome), suggest a level of distinction at the general community level. The seeds of the majority of tree species with fleshy fruits in the savanna regions of central Brazil ($\sim 15\text{--}20^\circ$ S) are dispersed by zoochory and produced in the rainy season, when regional environmental conditions become ideal for fruit duration and seed germination (Gottsberger & Silberbauer-Gottsberger 1983, Batalha *et al.* 1997, Antunes & Ribeiro 1999, Batalha & Mantovani 2000, Weiser & Godoy 2001, Batalha & Martins 2004, Lenza & Klink 2006).

Tree species located in environments beyond $\sim 15^\circ$ (N or S) may have different patterns and syndromes. In this particular geographical range, photoperiod climatic variations vary greatly in comparison with typical equatorial regions (Borchert *et al.* 2005). The rainy season in these latitudinal areas, which are farther away from the equator than our study area, coincides with the highest level of daily irradiance, potentially resulting in better photosynthetic yields and acting as a stimulus for reproductive events (Wright & Schaik 1994, Hamann 2004, Stevenson *et al.* 2008). In contrast, the dry season (winter) is cold and inhibits the formation of flower buds for the majority of plant species. At the latitudinal range where our research was carried out (2° to 3° N), the dry season corresponds with low amounts of cloud cover and the highest possible number of effective irradiance hours (see Fig. 1). On the other hand, in the rainy season, the local savannas are subject to the highest levels of cloud cover which, in turn, reduces the effective number of hours of light per day. In the Amazon region, the "latitude effect" acts directly on the amount of rainfall and radiation received by the different ecosystems within the region (Bradley *et al.* 2011), implying that latitudinal differences can determine the climatic control over phenological events (Zhang *et al.* 2004). In this way, we suggest that the reproductive phenophases of our study species indicate that the stimulus for initiating reproductive events can be associated with low cloud cover, low rainfall, and high levels of sun exposure.

Foldats & Rutkis (1975) pointed to annual variations in the water table, as well as periodic fires and herbivory, as playing fundamental roles in the phenology of *C. americana*. All of these factors were observed in both our study areas, since reductions in regional rainfall cause soil moisture to drop. At the

end of the dry period, the probability of seedling establishment and survival by late fruits is greater than that of early fruits (Frankie *et al.* 1974, Justiniano & Fredericksen 2000). For example, both *B. coccolobifolia* and *B. crassifolia* have small proportions of late reproductive events (beginning of the rainy season) for the areas sampled in Roraima. The ripening of these fruits at the end of the dry season and the beginning of the rainy season could increase the probability of seedling germination and growth due to an increase in soil moisture, temporary abundance of nutrients, and potential for deeper rooting (Schaik *et al.* 1993, Felfili *et al.* 1999).

For *B. coccolobifolia*, the association between reproductive events and rainfall was not as clear as in the other two species due to the second flowering peak at the beginning of the rainy season. The annual double-flowering strategy of this particular species was also observed in the Alter do Chão savanna in the state of Pará, although, in contrast to Roraima, the higher peak was in the rainy season and the lower was in the dry season (Miranda 1995). This difference may be explained by the ecological divergence between populations of the same species, which can lead to a distinct synchrony in sympatric species (Barros 2002). On the other hand, this could indicate variability in environmental stimuli (e.g. more accentuated seasonality or fire) in geographically separated savanna regions. For *B. coccolobifolia* in Roraima, the main peak of reproductive events precedes the natural leaf abscission process during the dry season. A smaller, secondary reproductive peak appears to be associated with the leaf renewal process that occurs just before the beginning of the rainy season. This double flowering process has also been observed by Benezar & Pessoni (2006), demonstrating that fire can accelerate the leaf abscission process and, as a consequence, stimulate new flowering.

The duration of the reproductive events of the three species, as a group, totaled 180–270 days throughout the year, although each individual phenophase spanned smaller periods of time (35–80 days). In a study on the phenology of seven species of *Byrsonima* in the Brasília savanna (Brazilian Central Plateau), the flowering period of *B. coccolobifolia* was estimated at 60 days (Barros 1992), a period of time 80% longer than that recorded for the same species in Roraima (~ 35 days). Furthermore, the fruit formation period can vary greatly, especially for *Byrsonima* spp. since the fruiting process can last up to four months, depending on the natural habitat in

question (Teixeira & Machado 2000). The duration of the reproductive events may be related to uncertainty in the pollination process (Rathcke & Lacey 1985). The three species studied in the Roraima savanna have a reproductive strategy of the most extensive flowering being synchronized with the dry season. This strategy can increase the likelihood of attracting pollinators and seed dispersers (Janzen 1967, Rathcke 1983). *Byrsonima crassifolia* (annual/evergreen) and *B. coccolobifolia* (sub-annual/brevi-deciduous) have small and fleshy fruit to attract birds that disperse the seeds at the end of the dry season (Ramírez 1993). Although seed dispersal in *C. americana* (annual/evergreen) is also zoochorous, the seed aril serves as an attractant. Thus, we expect that seeds of fleshy fruits, or fruits with exposed arils, will have the best chance of being dispersed during the dry season, coinciding with the period of greatest bird reproduction in the Amazonian savannas (Sanaïotti & Magnusson 1995). The relationship between seed dispersal by birds and fruit production can be considered a consequence of selective pressure (Stiles 1977). Zoochory is the principal dispersal syndrome for the majority of trees and shrubs in Amazonian savannas (Vieira *et al.* 2002), and is the most efficient method in environments with high seasonal variability and regular fire hazards. In contrast, anemochoric and autochoric species in other Brazilian savanna regions have displayed signs of synchronized dispersal during the rainy season (Mantovani & Martins 1988).

Based on our results, we conclude that the reproductive events of *C. americana* and *B. crassifolia* are synchronized with the dry season. This period of the year has less cloud cover and more insolation (irradiance) compared with the rainy season. *Byrsonima coccolobifolia* has a less pronounced synchrony with the dry period because this species has a sub-annual cycle, displaying a secondary phenological peak at the beginning of the rainy period. The duration of the phenological phases is short when compared with other studies carried out in higher-latitude Brazilian savannas (cerrados). The phenological patterns and reproductive cycles of the three study species are similar to those observed in other savannas in Brazilian Amazonia and Venezuela.

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