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Phenology and dispersal syndromes of woody species in deciduous forest fragments of the Pantanal in Mato Grosso do Sul State, Brazil

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ABSTRACT

We analyzed the phenological responses of shrub-tree species of lowland deciduous (LDF) and submontane deciduous (SFD) forests in the Pantanal, and assessed their relationships with climatic factors at the community level and with strategies for seed dispersal. Vegetative and reproductive phenophases of 50 tree-shrub species were monitored monthly (12 months), and their relationship with climatic variables was tested using multiple linear regression. Time of leaf budding differed between areas for autochoric species and between autochoric and anemochoric species at LDF. Leaf fall in communities and functional groups was seasonal and highly synchronous during the dry season (95 % of species). Leaf budding peaked at the end of the dry season with > 80 % synchrony. In general, the species presented low synchrony or asynchrony for flowering phenophases, while fruiting phenophases were weakly seasonal but differed between functional groups. Temperature and precipitation were the regulating factors of vegetative phenophases in LDF, while daylength regulated them in SDF. Abiotic factors only influenced flowering phenophases at the dispersion group level. Only ripe fruits were related to reduced daylength. The phenophases of the deciduous forests of the Pantanal seem to be regulated not only by climatic factors but also by strong endogenous control.

Keywords: deciduous forest, functional groups, Pantanal, reproductive phenology, seed dispersion, vegetative phenology

Introduction

Studying periodic variation in the life cycle of plants and its correlations with regulatory factors is crucial for understanding the temporal dynamics of plant communities (Vasconcelos *et al.* 2010). Annual and sub-annual fluctuations of phenophases may indicate the environmental factors, both abiotic (e.g. precipitation) and biotic, that drive them, including interactions with pollinators, dispersers and herbivores (Morellato & Leitão-Filho 1992).

The complex phenological patterns found in Neotropical forests have led to many new concepts describing these oscillations (Newstron *et al.* 1994a, 1994b). While vegetative and reproductive activities in temperate forests are predominantly regulated by temperature and day length (Janzen 1980; Rathcke & Lacey 1985), several factors, such as precipitation (Morellato *et al.* 2000; Talora & Morellato 2000; Griz & Machado 2001), temperature (Ferraz *et al.* 1999), day length (Rivera *et al.* 2002; Valdez-Hernández *et al.* 2010) and soil water availability (Borchert 1999; Borchert *et al.* 2004; Córtes-Flores *et al.* 2017), interact and regulate the development of phenophases in the tropics.

In strongly seasonal environments, abiotic factors may force species to adjust to water availability due to limited periods favorable for leaf activity, flowering and fruiting (Deprá & Gaglianone 2018). Synchronization of leaf budding during the vegetative dry season can facilitate

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herbivory escape (Schaik *et al*. 1993) while the synchronous occurrence of flowering and fruiting can increase the amount of pollinators and dispersers among different species whose flowers and fruits have similar morphological characteristics, thus increasing the success of pollination and dispersal (Janzen 1967; Justiniano & Fredericksen 2000). However, the time and intensity of phenophases in a community may differ due to intrinsic factors of a species (*i.e.* phylogenetic characteristics), as well as the ecological group to which it belongs (Ferraz *et al*. 1999; Williams-Linera & Alvarez-Aquino 2016).

In general, deciduous forests exhibit remarkable seasonality, defined by Newstron *et al.* (1994b) as a restricted period of the year in which most species lose their leaves, bloom and fruit. Interactions between water availability, root system depth, stem water storage and stress sensitivity lead to a wide variety of phenological behaviors in these environments (Mooney *et al*. 1995). Edaphic factors (topography and slope) affect soil drainage patterns and, consequently, the vegetative and reproductive phenology of species in dry forests, which attempt to adapt to low soil water retention capacity, drought risk and overheating from increased evapotranspiration rates (Borchert *et al.* 2004; Méndez-Toribio *et al*. 2017).

Leaf fall for trees and shrubs is a typical phenological pattern in deciduous seasonal forests that allows plants to escape water stress in the driest period of the year (Singh & Kushwaha 2016), however, in general, species possess different flowering and fruiting strategies depending on their functional group (Valdez-Hernández *et al.* 2010). The classification of species into functional groups, such as dispersal syndromes, may help in the comparison of results for similar ecosystems and to understand the behaviors of a group of species (Valdez-Hernández *et al.* 2010). Since seed dispersion is fundamental for the distribution and diversity of species in a community (Williams-Linera & Alvarez-Aquino 2016), fruiting may occur during the rainy season or at the end of the dry season, so that the diaspore develops in favorable environmental conditions (Janzen 1967; Frankie *et al*. 1974; van Schaik *et al.* 1993; Griz & Machado 2001; Williams-Linera & Alvarez-Aquino 2016). For example, in markedly seasonal ecosystems, zoochoric species show peak fruiting in the wettest season of the year (Cortés-Flores *et al*. 2018). In turn, autochoric and anemochoric species exhibit fruitification peaks in drier periods of the year, which are conducive to fruit ripening by dehydration and subsequent wind dispersal (Pirani *et al*. 2009).

The main continuous areas of Neotropical dry forests are located in northeastern Brazil, with Caatinga vegetation, and in southeastern Bolivia, Paraguay and northeastern Argentina, with typical Chaco vegetation (Valdez-Hernández *et al.* 2010). At the Brazil/Bolivia border, in the residual relief hills on the western border of the Pantanal, deciduous forest remnants present floristic elements similar to northeastern Caatinga, the Chaco and the Chiquitano dry forest of Bolivia (Prado & Gibbs 1993; Damasceno-Junior *et al.* 2018). These fragments are located in a non-flooded area, and therefore serve as a refuge for wild animals and cattle during flood periods in the Pantanal (Salis *et al.* 2004).

Despite the high beta diversity found in deciduous seasonal forests (Linares-Palomino *et al.* 2011), these forests on the western border of the Pantanal are still poorly studied due, in part, to their occurrence in areas of intense anthropogenic disturbance caused by urbanization, livestock, settlements and mining (Salis *et al*. 2004; Damasceno-Junior *et al.* 2018). Only two phenological studies about plant communities have been carried out in the region of the Urucum massif, one in deciduous forest and the other in Cerrado grasslands with ferruginous soil (Ragusa -Netto & Silva 2007; Neves & Damasceno-Junior 2011). The present study is the first complete phenological analysis of deciduous lowland and submontane forests at the western border of the Pantanal using functional groups with different dispersal syndromes.

We aimed to analyze the phenological responses of shrub-tree species in fragments of deciduous forest surrounding the Pantanal in the state of Mato Grosso do Sul, Brazil, and assess their relationship with abiotic factors (temperature, day length, and precipitation) at the community level and with ecological strategies for seed dispersal. Our questions were: (1) What are the phenological responses of these forests? (2) What abiotic variables trigger vegetative and reproductive phenophases in these areas? (3) How do phenological responses vary among species with different dispersal strategies? We hypothesized that vegetative phenological responses would be strongly related to abiotic factors such as precipitation and day length, with no difference between montane and submontane forests, but patterns of flowering and fruiting would differ between dispersal syndrome functional groups since these phenophases depend on strong endogenous control.

Materials and methods

Study areas

The study areas are located about 3 km west of the urban perimeter of the municipality of Corumbá (19º 01-02’ S and 57º 40-41’ W), Mato Grosso do Sul State, and are separated by about 500 m, between which the Ramon Gomes highway passes (Fig. 1). The region encompasses 241 ha of deciduous anthropic forest vegetation of the foothills and hillsides. The first area encompasses approximately 91 ha and is classified as lowland deciduous forest (LDF; IBGE 1992). The relief is smooth wavy with less than 2 % slope and altitudes ranging between 90 and 150 m, with few rocky clusters of limestone and a thicker soil layer of medium to small textured chernosol rendzico gravel in the stony phase (Spera *et al.* 1997; Okida & Anjos 2000). The second area encompasses approximately 150 ha and is classified as

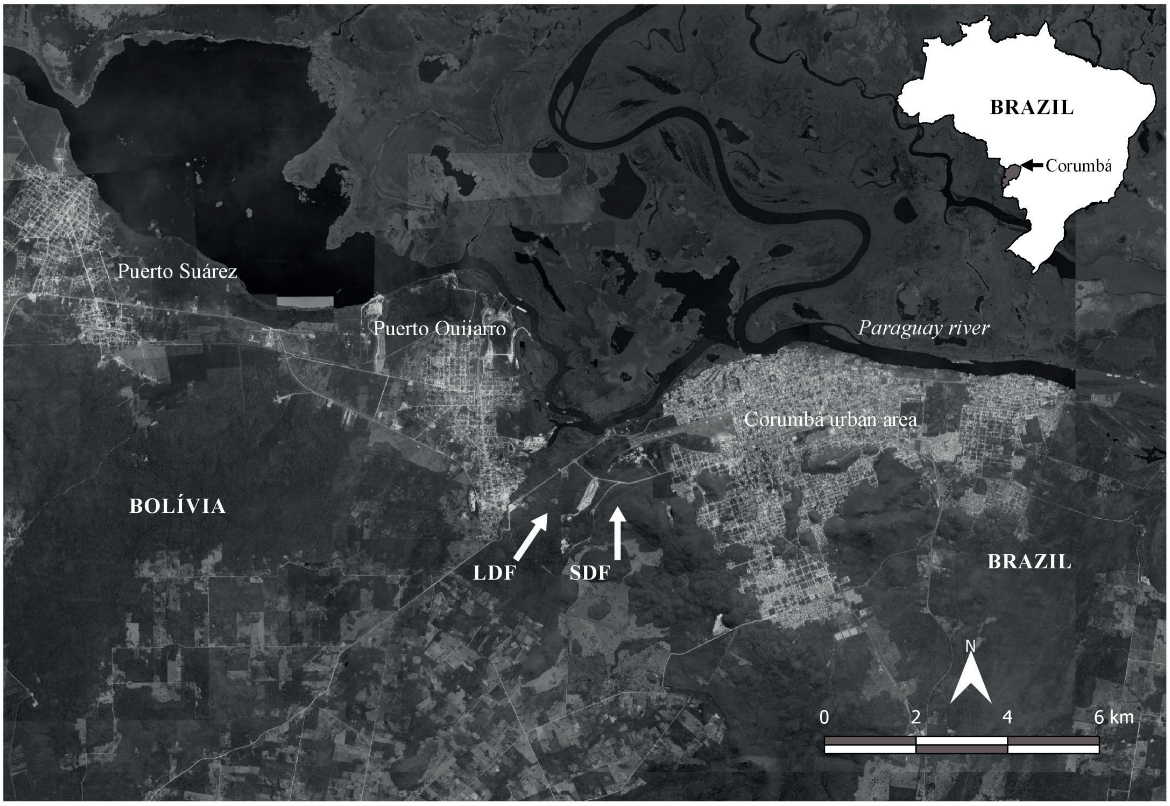

Figure 1. Location of the study area in the municipality of Corumbá, Mato Grosso do Sul. Arrows indicate sampling areas: LDF = lowland deciduous forest and SDF = submontane deciduous forest.

submontane deciduous forest (SDF; IBGE 1992). The soil is composed of medium-textured chernozenic eutrophic cambisol, with a strong rocky outcrop; the slope is between 20 % and 40 %, with altitudes ranging from 150 to 300 m (Spera *et al*. 1997; Okida & Anjos 2000).

According to the Köppen classification, the climate of the region is tropical with well-defined seasons (Aw), with rainy summers and dry winters (Alvares *et al*. 2013), and average annual temperature and precipitation of 25.1 °C and 1,070 mm, respectively (Soriano 1997). The rainy season occurs between November and March, and can reach 68 % of the total annual rainfall (> 110 mm/month), with average monthly temperatures ranging between 26 °C and 28 °C, and a maximum of 40 °C. In the dry season, which lasts from May to September, the average monthly temperatures fluctuate between 21 °C and 25 °C, and precipitation decreases considerably to < 60 mm/month (Soriano 1997). April and October correspond to transition periods between dry and rainy seasons. Temperature and average precipitation data were obtained from the Corumbá-MS Air Space Control Department and Agritempo site (2003), while day length data were obtained from On-line Photoperiod Calculator (Lammi 2001) (Fig.2).

The vegetation in both areas is characterized by predominantly caducipholic species, with more than 50 % of the individuals being devoid of foliage in the dry season. The deciduous forests on limestone deposits around the municipality of Corumbá have similar species as those of the Chiquitano dry forest of Bolivia (Jardim *et al*. 2003) and the seasonal forests of South America's Pleistocene

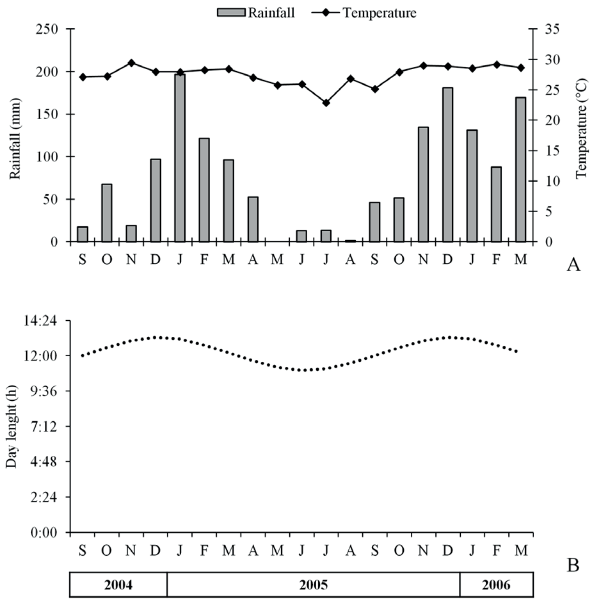

Figure 2. Climatic pattern for the municipality of Corumbá, Mato Grosso do Sul, from September 2004 to March 2006: **A.** distribution of annual rainfall and absolute average temperature; **B.** day length.

Arc, which includes northeastern Caatinga (Prado & Gibbs 1993). A phytosociological study conducted in the same areas indicated the predominance of *Acosmium cardenasii* H.S.Irwin & Arroyo, *Anadenanthera colubrina* (Vell.) Brenan, *Aspidosperma pyrifolium* Mart. & Zucc., *Aspidosperma quirandy* Hassl., *Calycophyllum multiflorum* Griseb., *Ceiba pubiflora* (A.St.-Hil.) K.Schum., *Cnidoscolus vitifolius* (Mill.) Pohl, *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Myracrodruon urundeuva* Allemão, *Pseudobombax marginatum* (A.St.-Hil., Juss. & Cambess.) A.Robyns and *Simira corumbensis* (Standl.) Steyerm., some of which are widely distributed and occur in similar Brazilian vegetation types (Lima *et al.* 2010).

Data collection

To monitor the phenophases of leaf budding, leaf fall, floral buds, flowers at anthesis, unripe fruits and ripe fruits, 20 sampling points (separated from each other by 100 m) were marked in each forest area (LDF and SDF) along a 5 km x 4 m permanent trail. The first 15 trees and shrubs with circumference at breast height ≥ 15 cm were selected at each point. All individuals were marked with numbered aluminum plates and monitored monthly from February 2005 to January 2006 using binoculars (Fournier & Charpantier 1975).

For identification purposes, samples of the species, fertile and non-fertile, were collected and subsequently deposited in the COR herbarium (UFMS-CPAN). Taxa names followed the classification system of the Angiosperm Phylogeny Group (APG IV 2016), while the spelling of the names was confirmed by consulting the databases of Flora do Brasil 2020 (2020) and The Plant List (2013). The species were classified into seed dispersal syndromes (Pijl 1972), through field observations and the literature, to analyze the relationship between these ecological strategies and their phenological responses.

Data analysis

Four different methods of data analysis were employed. (1) Fournier Index: To estimate the intensity of each phenophase, phenological data were converted into a percentage of phenophase intensity (abundance method of Fournier), for which a scale of five categories was established ranging from zero to four, with intervals of 25 % between categories (Fournier 1974; Bencke & Morellato 2002a; D'Eça-Neves & Morellato 2004). The sum of the values obtained for all individuals of each species per month was subsequently divided by the maximum possible value (number of individuals observed multiplied by four), with the result being multiplied by 100 to get a percentage (Bencke & Morellato 2002a). (2) Activity Index: This index is a qualitative method to estimate synchrony among individuals of a population or among species of a community. It consists of a presence/absence record of a phenophase observed for each individual and species in each month, with the values obtained for individuals/species who expressed a certain phenophase being summed and divided by the total number of individuals/species sampled for each area, followed by multiplying by 100 to get a percentage (Bencke & Morellato 2002b; D'Eça-Neves & Morellato 2004). Synchrony among all individuals and species was also calculated for comparison. Analysis of population and community synchrony considered the phenophases of leaf budding (shoots and young leaves), leaf fall (total absence of leaves or less than 50 % in the crown, or change in leaf color followed by senescence), flowering (floral buds and flowers at anthesis) and fruiting (unripe and ripe fruits). Phenological activity was considered asynchronous when < 20 % of the individuals or species presented the phenophase, lowly synchronous when 20-60 % of the individuals or species presented the phenophase, and highly synchronous when > 60 % of the individuals or species presented the phenophase (Bencke & Morellato 2002b). (3) Months were converted to angles, from 0° = January to 330° = December, with 30° intervals. The number of species in each phenophase for each angle was used to test seasonality, which was assessed at the community level and according to dispersal strategy. The following were calculated: mean angle ($\bar{a}$), which indicates the average date of phenophase activity; standard deviation; and vector length (r), which represents the concentration of phenological data, ranging from 0 (no seasonality) to 1 (all species showing the phenophase at the same time) (Morellato *et al*. 2010). Rayleigh's test was used to assess the significance of the mean angle (Zar 1996). The null hypothesis was that the data is uniformly distributed throughout the year, with no concentration around the mean angle, which would indicate absence of seasonality (Morellato *et al.* 1989; Zar 1996; Nanda *et al*. 2014). In cases where seasonality was confirmed (*i.e.* $p < 0.05$ and the vector was the above 0.2 threshold; Valentin-Silva *et al*. 2018), the Watson-Williams (F) test was applied to test whether the mean angles of phenophases differed among dispersion groups and for the same syndrome between areas. (4) Multiple linear regression was used to test for relationships between phenophases and abiotic variables (precipitation, day length, and temperature), with the best models being selected using Akaike information criterion (AIC; Crawley 2007). The frequency of species per forest type and dispersion type showing the phenophase was considered the response variable, and monthly means of abiotic variables were the explanatory variables. Since phenological responses can occur late after the manifestation of environmental stimuli, climatic data were considered from the month of phenophase occurrence until two months prior (November 2004). All analyses were conducted using R (R Core Team 2019), with the functions *lm* and *stepAIC* (Venables & Ripley 2002) of the MASS package being used to find the best models. A significance level of 5 % was used for all analyses.

Results

A total of 595 individuals of 50 species and 24 families were sampled, with 298 individuals of 42 species in LDF and 297 individuals of 40 species in SDF (Figs. S1 and S2 in supplementary material). The number of sampled individuals ranged from one to 41 per species. Only one species, of the family Myrtaceae, could not be identified beyond the family level.

Vegetative phenology

The pattern of vegetative activity in both areas was similar, with marked seasonality (Figs. 3, 4). Species (> 30 %) began to lose their leaves in May at the beginning of the dry season, with peak leaf fall (> 90 %) at the end of the dry season in September (Figs. 3A, 4A). Leaf fall was also highly synchronous among individuals in September (> 90 %; Figs. 3B, 4B). The intensity of leaf fall coincided with the drier months (July to September) and decreased day length in both areas (Fig. 2), and peaked in September (Figs. 3C, 4C). Synchrony of leaf budding was similar between the communities of the two areas, with it peaking at the end of the dry season (> 80 %; Figs. 3A, 4A). Although the percentage of individuals exhibiting leaf shoots was lower than for the species level, synchrony was above 70% (Figs. 3B, 4B). The intensity of leaf budding was < 40 % in both areas (Figs. 3C, 4C). When analyzed by dispersion strategies (Fig.5), anemochoric and zoocoric species showed little synchrony (between 30-50 %) for vegetative phenophases, while autocoric species were asynchronous (< 20 %) (Fig. 5A-B, E-F).

Circular analysis at the community level and by dispersion mode indicated that the leaf fall and leaf budding were significantly seasonal in the two sampled areas, with a large concentration of activity around the mean angle (*r* > 0.6, Tab. 1). The activity of leaf buds in LDF and SDF was concentrated in September (Tab. 1), a period characterized by the onset of rainfall and an increase in day length (Fig. 2). Similarly, the average date of leaf fall was in July, middle of the dry season (Tab. 1). Among the dispersion groups, there was a difference

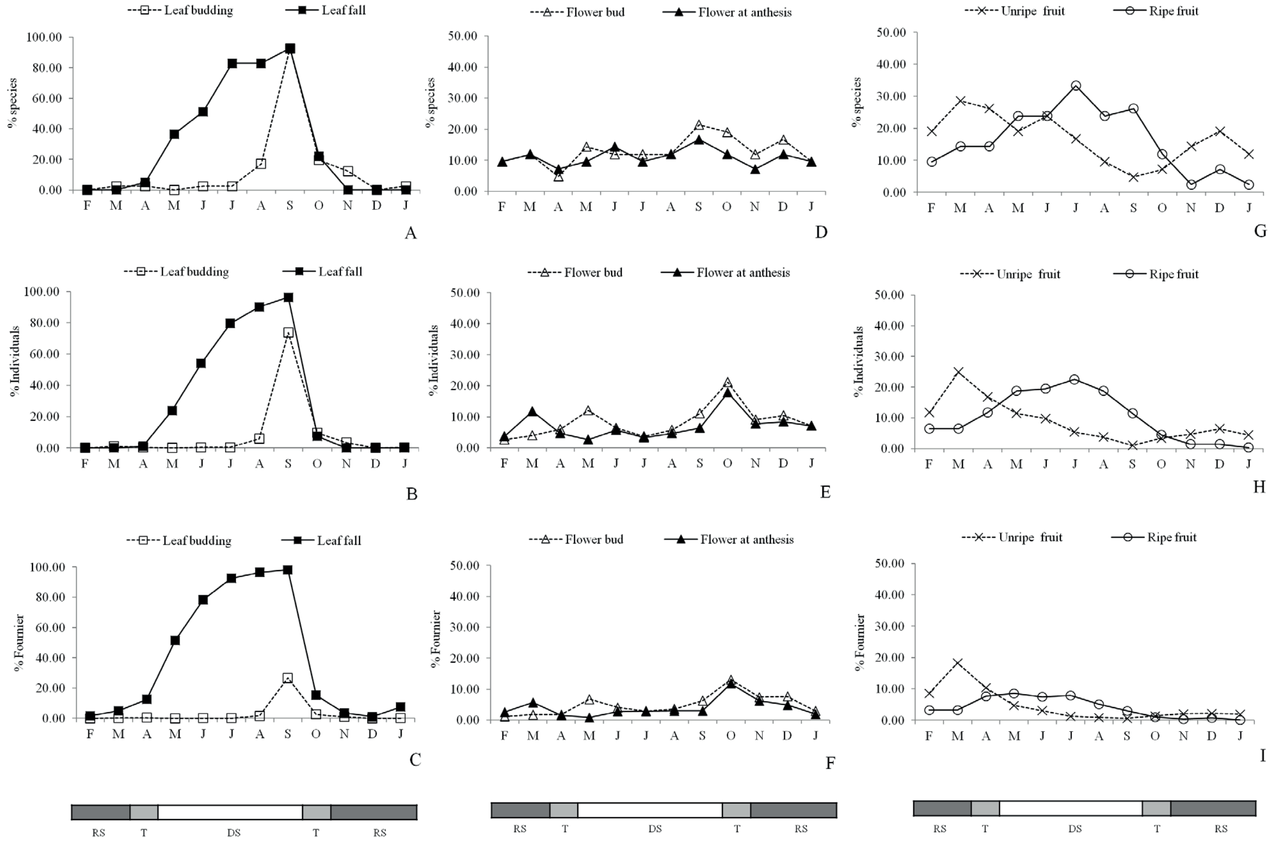

Figure 3. Phenology of tree-shrub species of a lowland deciduous forest in Corumbá, Mato Grosso do Sul, from February 2005 to January 2006. **A.** Percentage of species exhibiting vegetative phenophases. **B.** Percentage of individuals exhibiting vegetative phenophases. **C.** Intensity of vegetative phenophases. **D.** Percentage of species exhibiting reproductive phenophases (floral buds and flowers at anthesis). **E.** Percentage of individuals exhibiting reproductive phenophases (floral buds and flowers at anthesis). **F.** Intensity of reproductive phenophases (floral buds and flowers at anthesis). **G.** Percentage of species exhibiting reproductive phenophases (unripe and ripe fruit). **H.** Percentage of individuals exhibiting reproductive phenophases (unripe and ripe fruit). **I.** Intensity of reproductive phenophases (unripe and ripe fruit). RS = rainy season, T = transition between seasons, DS = dry season.

in the mean angle only for the leaf budding phenophase of autochorous species between areas (F = 7.676, $p < 0.05$) and between autochorous and anemochorous species of LDF (F = 6.782, $p < 0.05$). Phenophases were related to at least one abiotic variable during the month of occurrence or in the previous months, both by area and by dispersion strategies. Leaf budding had a negative relationship with mean temperature two months prior to the occurrence of the phenophase only in LDF (Tab. 2) and was not related to any abiotic variable in SDF (Tab. 3). By dispersal strategy, the reduction of rainfall in the month of occurrence of the phenophase was the predictor variable for autochoric species of LDF. There were no significant results for zoochoric species of LDF, autochoric species of SDF, and for anemocoric species in general. Although statistically significant, the results for zoochoric species at SDF were not conclusive.

Leaf fall for anemochoric and autochoric species of LDF (Tab. 2) was associated with reduced temperature (time-lag 1) and rainfall (time-lag 2), respectively. There were no significant results for zoochoric species of LDF. Leaf fall for autochoric and zoochoric species of SDF responded to variation in day length in the month of occurrence of the phenophase and one month prior (Tab. 3). For the other analyses, the selection of multiple regression models using AIC was not sufficiently simplified to explain the triggering of leaf fall in both areas.

Reproductive phenology

The species *Cordia glabrata*, *Coutarea hexandra* and *Pereskia sacharosa* in LDF, and *Pisonia zapallo* and *Phyllostylon rhamnoides* in SDF, did not flower or fruit during the study period. *Amburana cearensis*, *Bougainvillea infesta* and Myrtaceae 1 also did not show reproductive activity in both areas. These species represent about 3.02 % and 8.75 % of all individuals sampled in the LDF and SDF, respectively. The absence of reproductive activity may indicate that the selected individuals were not at reproductive stage, or that these species possess a supra-annual reproduction pattern, not detected in the single year of the present study.

In both areas, the species presented low synchrony (between 20-30 %) or asynchrony (< 20 %) of floral buds

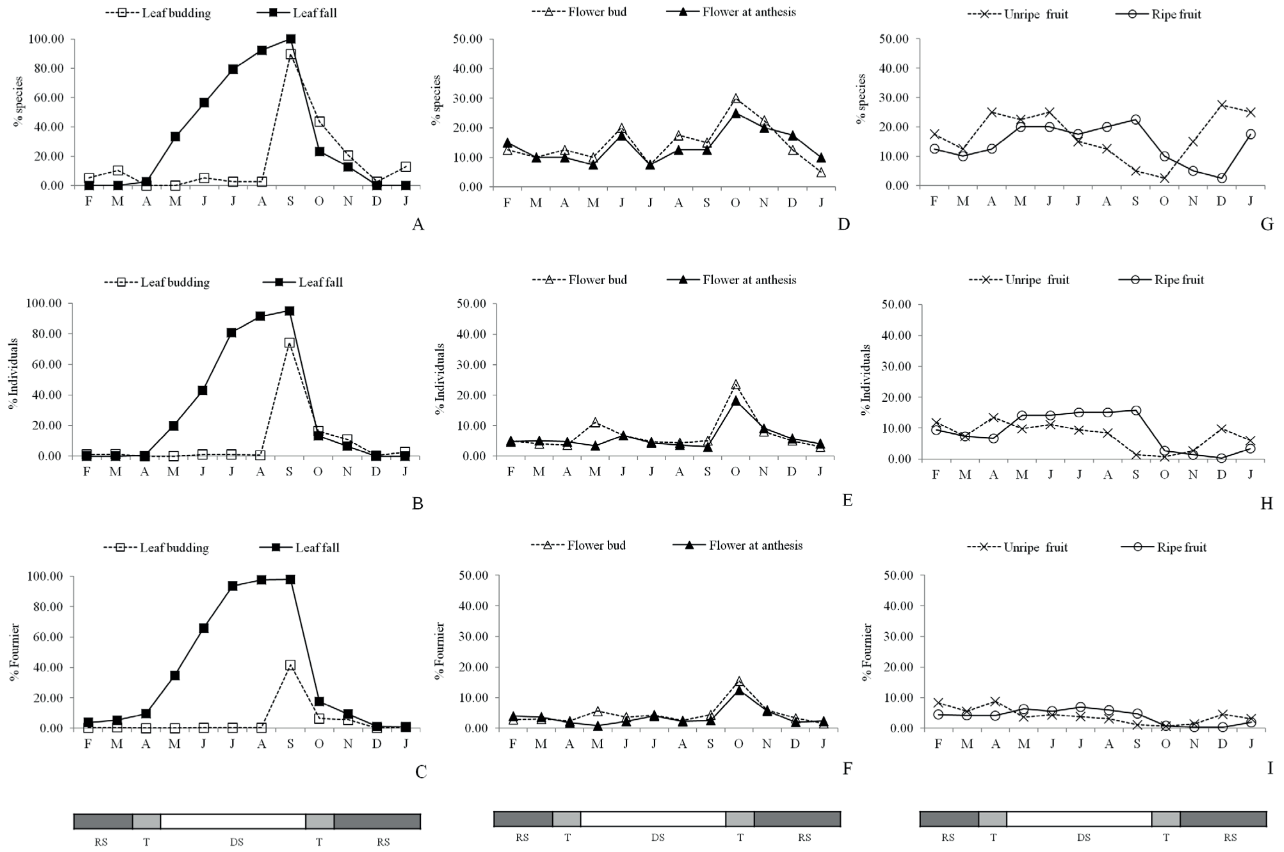

Figure 4. Phenology of tree-shrub species of a submontane deciduous forest in Corumbá, Mato Grosso do Su, from February 2005 to January 2006. **A.** Percentage of species exhibiting vegetative phenophases. **B.** Percentage of individuals exhibiting vegetative phenophases. **C.** Intensity of vegetative phenophases. **D.** Percentage of species exhibiting reproductive phenophases (floral buds and flowers at anthesis). **E.** Percentage of individuals exhibiting reproductive phenophases (floral buds and flowers at anthesis). **F.** Intensity of reproductive phenophases (floral buds and flowers at anthesis). **G.** Percentage of species exhibiting reproductive phenophases (unripe and ripe fruit). **H.** Percentage of individuals exhibiting reproductive phenophases (unripe and ripe fruit). **I.** Intensity of reproductive phenophases (unripe and ripe fruit). RS = rainy season, T = transition between seasons, DS = dry season.

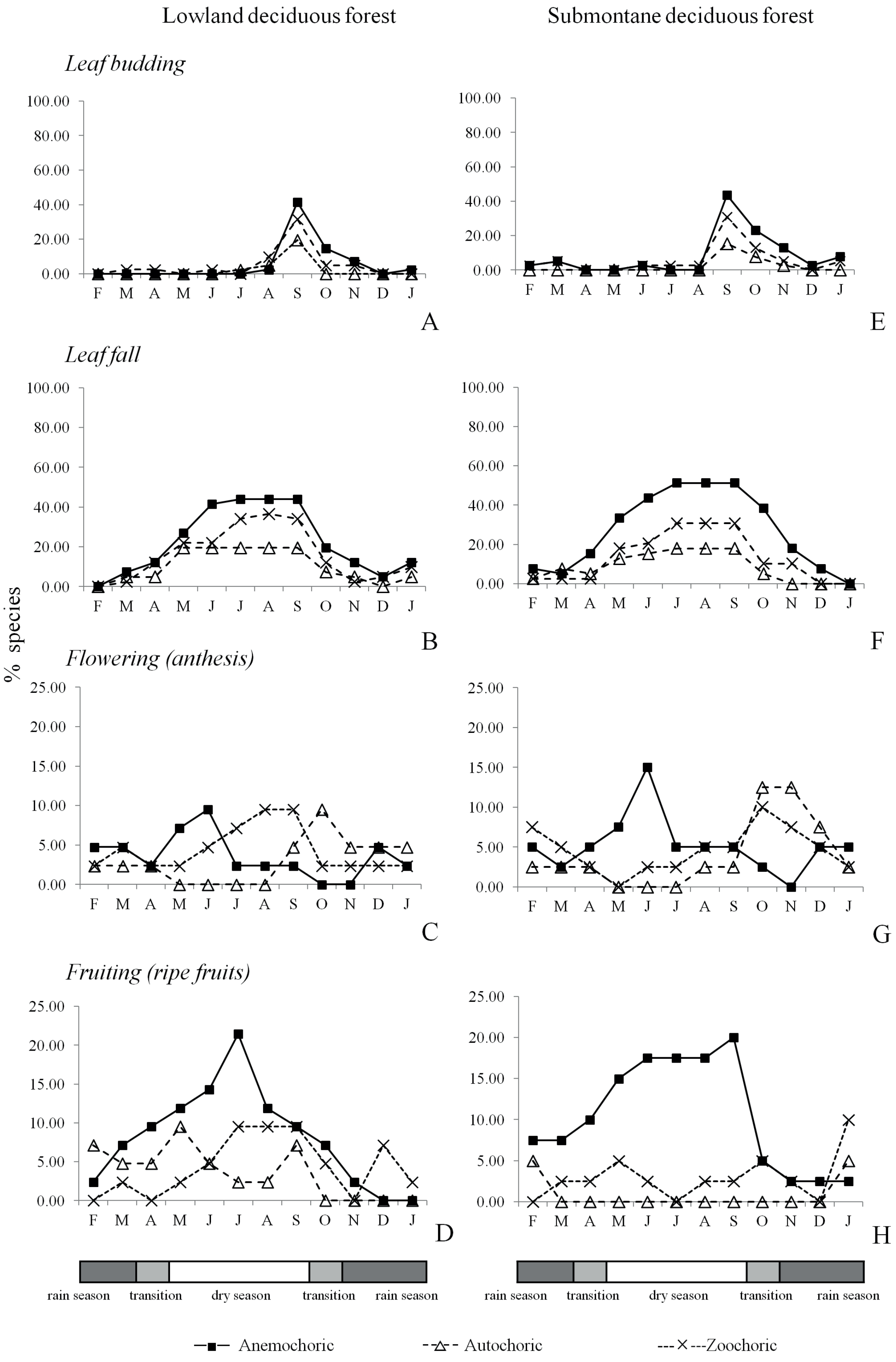

Figure 5. Percentage of species exhibiting vegetative and reproductive phenophases, grouped by dispersion strategy (anemochory, autochory, and zoochory), in lowland and submontane deciduous forests, Corumbá, Mato Grosso do Sul. Lowland deciduous forest: **A.** Leaf budding. **B.** Leaf fall. **C.** Flowering (flower at anthesis). **D.** Fruiting (ripe fruits). Submontane deciduous Forest. **E.** Leaf budding. **F.** Leaf fall. **G.** Flowering (flower at anthesis). **H.** Fruiting (ripe fruits).

Table 1. Results of circular statistical analysis of lowland and submontane deciduous forests, for the phenophases of leaf budding, leaf fall, floral buds, flowers at anthesis, unripe fruits, and ripe fruits for **A.** all species together, and **B.** species grouped by dispersal syndrome. (minimum level of significance: $r > 0.2$, $p < 0.05$). SD = standard deviation.

	Lowland deciduous forest						Submontane deciduous forest					
	Leaf budding	Leaf fall	Flower bud	Flower (anthesis)	Unripe fruits	Ripe fruits	Leaf budding	Leaf fall	Flower bud	Flower (anthesis)	Unripe fruits	Ripe fruits
A. All species together												
Mean angle (μ)	243.7° (sep)	197.2° (jul)	255.4°	221.6°	80.1° (mar)	171.0° (jun)	261.4° (sep)	201.8° (jul)	253.0°	289.9°	65.8° (mar)	164.7° (jun)
Lenght of mean vector (r)	0.82	0.74	0.16	0.08	0.26	0.39	0.66	0.72	0.19	0.17	0.2	0.22
Circular Standard Deviation	36.0°	44.5°	109.6°	129.2°	94.2°	78.5°	52.0°	46.1°	104.8°	107.4°	103.4°	100.3°
Rayleigh Z	42.5	83.7	1.7	0.34	5.6	12.4	33.3	81.5	2.5	2.0	3.2	3.2
p	<0.001	<0.001	0.187	0.712	0.004	<0.001	<0.001	<0.001	0.085	0.141	0.042	0.042
B. Seed dispersal mode												
Anemochorous												
Mean angle (μ)	253.9° (sep)	193.3° (jul)	91.5°	103.4°	116.3° (apr)	167.1° (jun)	267.5° (sep)	199.5° (jul)	136.9° (may)	139.1°	121.1° (may)	171.3° (jun)
Lenght of mean vector (r)	0.88	0.49	0.28	0.35	0.52	0.50	0.66	0.50	0.33	0.29	0.53	0.40
Circular SD	28.3°	68.8°	91.9°	83.3	65.8°	67.0°	52.0°	67.9°	85.5°	90.3°	64.7°	77.8°
Rayleigh Z	21.9	26.0	1.4	2.2	7.0	10.4	17.1	30.9	3.2	2.1	10.1	7.9
p	<0.001	<0.001	0.257	0.114	<0.001	<0.001	<0.001	<0.001	0.038	0.123	<0.001	<0.001
Autochorous												
Mean angle (μ)	229.7° (aug)	182.2° (jul)	310.9° (nov)	309.9° (nov)	34.8° (feb)	117.9° (apr)	254.6° (sep)	177.7° (jun)	283.8° (oct)	301.8° (nov)	2.0° (jan)	15° (jan)
Lenght of mean vector (r)	0.95	0.51	0.58	0.53	0.57	0.41	0.94	0.55	0.74	0.61	0.67	0.97
Circular SD	19.2°	66.7°	59.7°	64.6°	60.7°	76.0°	20.1°	62.9°	44.6°	57.1°	51.3°	15.1°
Rayleigh Z	9.8	13.1	5.7	4.2	8.5	3.1	8.8	12.0	9.3	7.0	9.4	3.7
p	<0.001	<0.001	0.002	0.012	<0.001	0.043	<0.001	<0.001	<0.001	<0.001	<0.001	0.012
Zoochorous												
Mean angle (μ)	237.5° (aug)	191.9° (jul)	221.2° (aug)	202.9°	160.9°	219.4° (aug)	255.4° (sep)	197.9° (jul)	272.9°	300°	318.4°	355.7°
Lenght of mean vector (r)	0.72	0.51	0.35	0.32	0.08	0.45	0.60	0.60	0.31	0.29	0.13	0.13
Circular SD	46.2°	66.3°	83.3°	86.6°	127.9°	72.7°	60.8°	57.8°	87.8°	89.7°	116.5°	116.5°
Rayleigh Z	12.5	20.7	3.7	2.2	0.2	4.4	8.8	22.4	2.2	1.9	0.4	0.2
p	<0.001	<0.001	0.022	0.106	0.806	0.011	<0.001	<0.001	0.111	0.15	0.675	0.805

and flowers at anthesis during the study period (Figs 3, 4). Flowering activity in LDF peaked at the end of the dry season in September, with 21 % of the species with floral buds and 16 % with flowers at anthesis. The peak of these phenophases in SDF occurred one month later, in October, which is the transition from the dry season to the rainy season, with 30 % of the species with floral buds and 25 % with flowers at anthesis (Figs. 3D, 4D). In both areas, October was also the period of highest activity considering all individuals together (Figs. 3E, 4E), and abundance of floral buds and flowers at anthesis (Figs. 3F, 4F). Analyzing these patterns by dispersal strategy (Fig. 5) revealed that the small peak of flowering at the beginning of the dry season was determined by the synchronized flowering of anemochoric species in both areas (Fig. 5C, G), namely the species *Ceiba pubiflora*, *Eriotheca roseorum, Handroanthus impetiginosus* and *Pseudobombax marginatum*. Then, in September (LDF) and October (SDF), maximum flowering activity (floral buds and flowers at anthesis) was observed for the zoochoric species *Commiphora leptophloeos* and *Jacaratia corumbensis*, and the autochoric species *Anadenanthera colubrina*, *Cnidoscolus vitifolius*, *Jatropha weddeliana* and *Sapium obovatum*. This period coincided with the onset of rainfall and increased day length in the study region (Fig. 2).

At the community level, seasonality of the phenophases of floral buds and flowers at anthesis was not significant for LDF and SDF (Tab. 1). For species grouped by dispersion strategies, only autochoric species presented seasonality for floral buds (LDF: $r = 0.58$, $p = 0.002$; SDF: $r = 0.74$, $p < 0.001$) and flowers at anthesis (LDF: $r = 0.53$, $p = 0.01$; SDF: $r = 0.61$, $p < 0.001$) (Tab. 1).

Multiple linear regression analysis using AIC was not significant for flowering phenophases (floral buds and flowers at anthesis) of all species together at LDF (Tab. 2). In turn, the selection of various regression models using AIC was not sufficiently simplified to explain the triggering of floral buds and flowers at anthesis in SDF (Tab. 3).

Table 2. Significant results of model selection of the possible variables responsible for triggering phenophases of the studied species in lowland deciduous forest. The complete model for calculating the relationships between explanatory variables and phenophases is given by the formula day2 + day1 + day0 + rain2 + rain1 + rain0 + temp2 + temp1 + temp0. Numbers after each variable refer to the time lag used in the analyses. AIC = Akaike information criterion; day = daylength; rain = rainfall; temp = mean temperature.

	AIC full model	Best model	AIC	Coefficients		F-value	p	Adj R^2
A. All species together								
Leaf budding	48.83	buddlow ~ temp2	45.24	Temp2	-6.825	5.62	0.04	0.71
Leaf fall	33.09	fallow ~ day2+rain1+temp2	29.95	Day2	-1.329	37.48	0.001	0.96
				Rain1	0.232			
				Temp2	-2.824			
Unripe fruits	11.18	unrilow ~ day2+day1+rain0	14.42	Day2	0.348	64.32	<0.001	0.98
				Day1	-0.492			
				Rain0	0.058			
Ripe fruits	15.36	riplow ~day1	9.89	Day1	-0.295	21.97	<0.001	0.90
B. Seed dispersal mode								
Anemochorous								
Leaf fall	18.38	anemofallow ~ temp1	12.72	Temp1	-1.902	39.78	<0.001	0.95
Flower (anthesis)	5.3	anemoflowlow ~ temp0	2.28	Temp0	-1.457	6.714	<0.05	0.51
Ripe fruits	7.22	anemoriplow ~ day1+temp0	10.48	Day1	-0.335	33.57	<0.01	0.95
				Temp0	1.312			
Autochorous								
Leaf budding	21.37	autobuddlow ~ rain0	15.13	Rain0	-0.091	3.853	<0.05	0.51
Leaf fall	15.83	autofallow ~ rain2	8.48	Rain2	-0.029	24.72	<0.001	0.87
Flower bud	1.25	autoflowbudlow ~ day0	8.51	Day0	0.026	10.35	<0.01	0.81
Flower (anthesis)	0.14	autoflowlow ~ day2+day0+rain1	6.69	Day2	0.105	6.511	<0.05	0.71
				Day0	0.082			
				Rain1	-0.036			
Zoochorous								
Flower bud	9.91	zooflowbudlow ~ day0+rain1	1.61	Day0	0.145	9.03	<0.01	0.69
				Rain1	-0.022			
Unripe fruits	17.69	zoounrilow ~ day2+day0+rain2+rain0+temp2	19.33	Day2	-0.316	11.32	<0.05	0.88
				Day0	-0.277			
				Rain2	0.028			
				Rain0	0.071			
				Temp2	0.730			
Ripe fruits	2.37	zooriplow ~ day2+day1	2.71	Day2	-0.162	6.89	<0.05	0.76
				Day1	0.201			

Table 3. Significant results of model selection of the possible variables responsible for triggering phenophases of the studied species in submontane deciduous forest. The complete model for calculating the relationships between explanatory variables and phenophases is given by the formula day2 + day1 + day0 + rain2 + rain1 + rain0 + temp2 + temp1 + temp0. Numbers after each variable refer to the time lag used in the analyses. AIC = Akaike information criterion; day = daylength; rain = rainfall; temp = mean temperature.

	AIC full model	Best model	AIC	Coefficients		F-value	p	Adj R^2
A. All species together								
Leaf fall	28.2	falsub ~ day2+rain1+temp2	26.21	Day2	-1.600	39.19	<0.01	0.96
				Rain1	0.197			
				Temp2	-3.608			
Flower bud	9.86	flowbudsub ~ day2+ day0+rain2+rain1+rain0 +temp1	5.19	Day2	0.183	11.57	<0.01	0.85
				Day0	0.065			
				Rain2	-0.060			
				Rain1	-0.103			
				Temp1	-1.156			
Flower (anthesis)	8.49	flowsub ~ day1+day0+rain2+rain1+ temp1	1.05	Day1	0.003	11.05	<0.01	0.83
				Day0	-0.115			
				Rain2	-0.050			
				Rain1	-0.100			
				Temp1	-1.592			
Ripe fruits	26.5	ripsub ~ day2+day1+day0+rain2+temp2+temp1+temp0	28.61	Day2	-0.717	141.8	<0.001	0.99
				Day0	-0.720			
				Rain2	0.025			
				Rain1	0.006			
				Rain0	0.002			
				Temp1	-0.818			
B. Seed dispersal mode								
Anemochorous								
Leaf fall	0.35	anemofalsub ~ day2+day1+day0+ rain2+rain1+rain0+temp2+temp1 +temp0	7.24	Day0	0.172	330.2	<0.001	0.99
				Rain1	-0.109			
				Temp1	-2.583			
				Temp0	-2.022			
Flower (anthesis)	6.53	anemoflowsub ~ day1+day0+rain1+temp1+temp0	9.06	Day1	0.191	8.237	<0.05	0.82
				Day0	-0.035			
				Rain1	-0.068			
				Temp1	-2.084			
				Temp0	-2.542			
Unripe fruits	36.79	anemounrisub ~ day1+day0+rain2+ rain1+rain0+temp2+temp1+temp0	36.79	Day1	0.359	142.8	<0.01	0.99
				Day0	-0.214			
				Rain2	0.020			
				Rain1	-0.058			
				Rain0	0.051			
				Temp2	0.468			
				Temp1	-1.695			
				Temp0	-1.719			
Autochorous								
Leaf fall	14.74	autofalsub ~ day1+day0	4.77	Day1	-0.248	24.29	<0.001	0.86
				Day0	0.158			
Flower bud	1.51	autoflowbudsub ~ rain2+temp1+temp0	7.08	Rain2	-0.026	17.23	<0.01	0.90
				Temp1	1.053			
				Temp0	0.908			
Flower (anthesis)	3.05	autoflowsub ~ day2+temp1	4.51	Day2	-0.024	12.62	<0.01	0.84
				Temp1	0.892			
Unripe fruits	14.6	autounrisub ~ day2+day1+day0	19.86	Day2	-0.261	60.13	<0.001	0.97
				Day1	0.521			
				Day0	-0.286			
Ripe fruits	22.59	autoripsub ~ day2+temp2+temp1	25.24	Day2	0.107	9.3	<0.05	0.84
				Temp2	-0.881			
				Temp1	-0.544			

Table 3. Cont.

	AIC full model	Best model	AIC	Coefficients		F-value	p	Adj R^2
Zoochorous								
Leaf budding	19.99	zoobuddsub ~ day2+day1+day0+rain2+rain0	16.01	Day2	0.845	6.464	<0.05	0.75
				Day1	-1.117			
				Day0	0.861			
				Rain2	-0.063			
				Rain0	-0.130			
Leaf fall	27.03	zoofalsub ~ day1+day0	16.11	Day1	-0.203	26.68	<0.001	0.87
				Day0	0.135			
Flower bud	12.88	zooflowbudsub ~ day0	14.53	Day0	0.336	10.39	<0.05	0.87
Ripe fruits	39.68	zooripsub ~ day1+day0+rain2+rain1+temp2+temp1	39.68	Day1	0.333	36.37	<0.05	0.97
				Day0	-0.187			
				Rain2	-0.046			
				Rain1	-0.044			
				Temp2	-0.548			
				Temp1	-0.942			

For anemochoric species, only the phenophase of flowers at anthesis was negatively related to mean temperature in the month of the occurrence of the phenophase in LDF (Table 2). For autochoric species, the association of flowering phenophases with climatic factors varied between areas. In LDF, the floral buds phenophase was positively related to day length (time-lag 0), while flowers at anthesis was positively associated with day length (time-lags 2 and 0) and negatively with rainfall 1 month before the occurrence of phenophase (Tab. 2). In SDF, autochoric floral buds was negatively associated with rainfall (time-lag 2) and positively with mean temperature (time-lag 1-0), while flowers at anthesis was associated with reduced day length (time-lag 2) and increased temperature one month prior (Tab. 3). For zoochoric species, only the floral buds phenophase was associated with climatic factors. In LDF, this phenophase responded to reduced rainfall one month prior and increase in day length in the month of occurrence (Tab. 2), while in SDF this phenophase responded to increased day length at time lag 0 (Tab. 3). Other analyses were not significant or not sufficiently conclusive.

Fruiting phenophases (unripe and ripe) were lowly synchronous among species (Figs. 3, 4), ranging from 20 to 33 %, with peak activity of unripe fruits in the rainy season and ripe fruits in the dry season in LDF (Fig. 3D). In SDF, the unripe fruit peak occurred in the rainy season in December and January and also in April (transition between seasons) and June (dry season). In turn, the peak of ripe fruits occurred at the end of the dry season in September, with a slightly lower peak in May–June, early dry season (Fig. 4D). In terms of individuals, fruiting activity was lowly synchronous in LDF, with unripe fruit peaking (24 %) in March, late rainy season, and ripe fruit peaking (22 %) in July, middle of the dry season, and asynchronous (< 20 %) in SDF (Figs. 3E, 4E). Fournier intensity analysis did not exceed 18 % for the presence of unripe and ripe fruit in both areas (Figs. 3F, 4F).

Considering the results for species dispersion strategies (Fig. 5), most ripe fruits observed during the dry season were supplied by anemochoric species, namely *Acosmium cardenasii*, *Aspidosperma* sp., *Calycophyllum multiflorum*, *Handroanthus impetiginosus* and *Simira corumbensis,* and a few individuals of autochoric and zoochoric species, such as *Cnidoscolus cnicodendron, Enterolobium contortisiliquum*, *Poincianella pluviosa* and *Sterculia striata* (Fig. 5D, H).

Unripe and ripe fruit phenophases were poorly seasonal in LDF, with a mean date in March ($r = 0.26$, $p = 0.004$) and June ($r = 0.39$, $p < 0.001$), respectively, both values with low concentration (Table 1). When analyzed by dispersal strategy, the significant mean angle of the event changed, with ripe fruit available for dispersal in June for anemochoric species ($r = 0.50$, $p < 0.001$), in April for autochoric species ($r = 0.41$, $p = 0.04$), and in August for zoochoric species ($r = 0.45$, $p = 0.01$), with low concentrations around the average date. The F-test found no significant differences between groups.

Unripe and ripe fruits phenophases were poorly seasonal in SDF, with an average date in March ($r = 0.2$, $p = 0.04$) and June ($r = 0.2$, $p = 0.04$), respectively, both values with low concentrations (Tab. 1). When analyzed by dispersion strategy, ripe fruit of anemochoric species was concentrated in June, during the dry season ($r = 0.40$, $p < 0.001$) and in January, the rainy season, for autochoric species ($r = 0.97$, $p = 0.01$). Fruiting (unripe and ripe fruits) of zoochoric species was not seasonal ($r = 0.13$, $p > 0.5$).

In general, only the ripe fruit phenophase of species in LDF was related to at least one abiotic variable, both by area and by dispersion strategy. Ripe fruit for all species was, in general, related to reduction in day length one month prior (Tab. 2). For anemochoric species this phenophase was associated with reduction in day length (time-lag 1) and increase of mean temperature in the month of occurrence (Tab. 2). Ripe fruit of zoochoric species (Tab. 2) had first a negative (time-lag 2) and then a positive (time-lag 1) relationship with day length. Other analyses were not significant or not sufficiently conclusive.

In general, most species showed deciduousness during the dry season, with the exceptions of *Anisocapparis speciosa*, *Capparidastrum coimbranum* and *Cynophalla retusa*, which are semideciduous species that progressively replaced senescent leaves with new leaves in the dry season. The species *Commiphora leptophloeos* and *Jacaratia corumbensis* produced buds and new leaves concomitantly with flowers during the dry season, shortly after leaf fall. In turn, trunk water storing species (*Ceiba pubiflora*, *Eriotheca roseorum*, *Pseudobombax marginatum*, *Myracrodruon urundeuva* and *Pisonia zapallo*) bloomed and fruited in the dry season with individuals totally stripped of foliage and leaf buds, which only appeared at the beginning of the rainy season. Other species, such as *Acosmium cardenasii*, *Calycophyllum multiflorum*, *Cnidoscolus vitifolius*, *Handroanthus impetiginosus*, *Helietta puberula*, *Poincianella pluviosa* and *Sterculia striata* flowered during the rainy season with fruiting extending throughout the dry season when totally stripped of foliage.

Discussion

The strongly seasonal vegetative activity, with leaf fall and leaf budding concentrated in the dry season, found here is similar to the pattern found by other studies conducted in deciduous forests around the world (Frankie *et al.*1974; Reich & Borchert 1984; Morellato 1992; Justiniano & Fredericksen 2000; Singh & Kushwaha 2016; Williams-Linera & Alvarez-Aquino 2016). Previous studies in deciduous forests of Brazil also found marked seasonality, with clear leaf fall in the drier period of the year (Griz & Machado 2001; Ragusa-Netto & Silva 2007; Vasconcelos *et al.* 2010; Dalmolin *et al.* 2015).

The soil of the municipality of Corumbá, where the study areas are located, is shallow with large limestone clusters (Lima *et al.* 2010). Woody species that grow in this region do not have immediate access to soil water supply, so they dehydrate long before losing their leaves (negative water potential) and do not rehydrate or produce leaves until the onset of the rainy season (Borchert 1999). Most species in the study areas remained leafless throughout the dry season, with new leaves emerging synchronously at the end of the dry season or shortly after the first rains. Tree species with strategies for water storage in the stem are common in seasonally dry environments, and include numerous species of Anacardiaceae, Burseraceae, Caricaceae, Euphorbiaceae, Malvaceae, and Fabaceae (Medina 1995), which were abundant families in the study areas. The low-density wood common in these species can potentially store large water reserves, which facilitates the break from dormancy by leaf buds (Rivera *et al.* 2002).

The foliar activity observed for the species in the study areas presented three patterns: (1) foliar activity induced by the first rains of the rainy season (deciduous species such as *Acosmium cardenasii*, *Amburana cearensis*, *Handroanthus impetiginosus, Jacaratia corumbensis*); (2) concomitant foliar activity and leaf fall during the dry season (semideciduous species such as *Anicocapparis speciosa*, *Capparidastrum coimbranum* and *Cynophalla retusa*); and (3) foliar activity that coincides with the longer day length after the spring equinox (deciduous species such as *Cordia brasiliensis*, *Myracrodruon urundeuva* and *Cedrella fissilis*, and succulent-stem species such as *Ceiba pubiflora*, *Eriotheca roseorum* and *Pseudobombax marginatum*). In general, there was predominance of species that produced leaf buds with the onset of rainfall in September and October, which coincides with the classification proposed by Borchert *et al.* (2004).

Significant relationships were found between vegetative phenophases and all climatic variables, although the results for the leaf fall phenophase were not statistically conclusive for both areas. In general, in heavily seasonal environments, short-term environmental events, such as changes in day length, temperature and variation in precipitation, which directly affect soil water storage, are indicated as triggering factors for vegetative phenophases (Reich & Borchert 1984; Frankie *et al.* 1974; Rivera *et al.* 2002; Singh & Kushwaha 2016). The trend of decreasing rainfall observed in the dry season reduces soil water availability, which forces species to lose their leaves to reduce water loss by evapotranspiration, while adjusting their reproductive phases to more favorable periods of the year (Reich & Borchert 1984). In turn, day length seems to be an independent phenomenon that induces synchronization throughout populations (Rivera *et al.* 2002). Despite being seemingly endogenously adjusted to avoid desiccation, this leaf phenological behavior can be adjusted to local environmental conditions.

Flowering was aseasonal for both areas and by dispersal strategy, except for authochoric species. In general, the species presented low synchrony or asynchrony in the activity of floral buds and flowers at anthesis. These results differ from other studies conducted in other seasonal deciduous forests (Justiniano & Fredericksen 2000; Ragusa-Netto & Silva 2007; Vasconcelos *et al.* 2010; Luna-Nieves *et al.* 2017), but similar to the results found in other dry tropical forests (Williams-Linera & Alvarez-Aquino 2016). Some authors hypothesize that the flowering period is determined by the rhythm of vegetative phenology, depending indirectly on environmental periodicity (Rivera *et al.* 2002; Borchert *et al.* 2004; Singh & Kushwaha 2016), and that leaf loss may result in stem rehydration followed by flowering (Singh & Kushwaha 2016). This was evident for some species of the present study, such as *Ceiba pubiflora*, *Handroanthus impetiginosus*, *Myracrodruon urundeuva* and *Tabebuia impetiginosa*, which flowered with the onset of the dry season (May), as soon as the leaves began to fall. Other species, such as *Casearia gossypiosperma*, *Commiphora leptophloeos*, *Enterolobium contortisiliquum*, *Erythroxylum pelleterianum* and *Guapira* sp., flowered after a full leaf fall at the end of the dry season in September, or during the transition from dry to rainy season in October, when the first leaves began to sprout. To prevent leaves and flowers from competing for water, nutrients and metabolites, trees may exhibit temporal separation between foliage and flowering, which may result in different flowering patterns in dry tropical forests (Borchert *et al*. 2004; Singh & Kushwaha 2016).

Some species, such as *Commiphora leptophloeos* and *Jacaratia corumbensis*, flowered and fruited simultaneously for a short period of time in the dry season, with the canopy covered with numerous leaf buds and young leaves but without leaf expansion, similar to the pattern observed in other studies (Frankie *et al.* 1974). One possible explanation is that this behavior may have evolved to facilitate locating flowers by pollinators. Another explanation is that simultaneous foliar activity can allow the species to continue to compete for light while flowering during long dry periods (Frankie *et al.* 1974). Since some of these species have a succulent stem or xylopodium for water storage (Lima *et al*. 2010), they can tolerate low soil water availability during the dry season, and thus can invest in the activities of flowering and fruiting while developing leaves.

Small flowering peaks observed in both areas are due to the activity of anemochoric and autochoric species at the beginning and end of the rainy season. In turn, synchronous flowering during the dry season, observed in some anemochoric species, could be an adaptation to water deficit (Mooney *et al.* 1995). For populations of *Handroanthus ochraceus* in deciduous forests, only when leaves are completely lost is water stress sufficiently reduced to allow partial anthesis under continued drought (Reich & Borchert 1982). On the other hand, the large number of flowers at anthesis in a short period of time would facilitate pollen flow among individuals and would reduce pollinator flight time and effort needed to search for resources (Janzen 1967; Rathcke & Lacey 1985; van Schaik *et al.* 1993; Frankie *et al.* 1974).

Except for flower buds of anemochoric species and flowers at anthesis of zoochoric species from both areas, and flowers at anthesis of anemochoric species at SDF, flowering was related to all climatic variables, influencing the onset of phenophases months prior and in the month of their occurrence. The relationship between flowering and climatic factors has also been documented for other seasonal tropical ecosystems, such as the deciduous forests of Mexico (Cortés-Flores *et al.* 2017), and the Cerrado (Batalha & Martins 2004; Pirani *et al.* 2009; Azevedo *et al.* 2014), and the pattern found by dispersal strategy is similar to that found by Williams-Linera & Alvarez-Aquino (2016). The species in these forests are mainly regulated by rainfall and soil water availability, which would be the main and essential causes of flowering by species at the community level, while the presence of pollinators and dispersers would play a small role in an environment poor in species and with the predominance of anemochoric seeds (Borchert *et al.* 2004).

Most of the species fruited in the driest period of the year, which is explained by the large number of species with anemochoric diaspores in the drier period of the year, typical of deciduous forests (Griz & Machado 2001; Cortés-Flores *et al*. 2018). Anemochoric diaspores are possessed by species of several families present in deciduous forests, such as Malvaceae, Apocynaceae, Leguminosae (Fabaceae), Bignoniaceae and Combretaceae, which were common botanical families in the areas of the present study (Lima *et al*. 2010). This type of syndrome involves little investment in fruits and seeds and there is no dependence on animal vectors (Janzen 1980). Zoochoric species also fruit predominantly in the driest period of the year, and produce fruits that are easily dispersed by local fauna; moreover, species that have continuous fruiting throughout the year may favor the maintenance of a local frugivore fauna, especially during more unfavorable periods when resources are scarce (Snow 1965). In turn, fruiting in autochoric species takes a long time to develop. Fruits remained on parent plants for a variable amount of time (three-nine months), which represents an ecological strategy to maintain seeds until they are viable for dispersion before the next rainy season (Luna-Nieves *et al*. 2017). Since the flowering peak of these species occurred at the end of the dry season, the fruits spent the entire rainy period in development and were finally ripe during the dry season, when the opening of fruit for seed dispersion is facilitated by decreased moisture (Batalha & Martins 2004). In all cases, the flowering and fruiting periods observed for the analyzed groups channel to the best period for seed germination, that is, in the rainy season (Rathcke & Lacey 1985).

Only the ripe fruit phenophase was related to climatic factors, although these relationships sometimes proved to be antagonistic between time-lags for the same phenophase. In forests with environmental stress, seed germination is generally limited by strong water restriction and high predation rates, which compromises the regeneration of vegetation throughout the year. Fruiting activity before the start of the rainy season or at the end of the next rainy season ensures that seedlings will have greater chances of receiving sufficient sunlight for development, and will have the entire rainy season to expand their root system before the start of the dry season (Janzen 1967).

The present study found little variation in phenological responses in deciduous forests located in different topographic conditions. Many species exhibited patterns similar to populations found in other seasonal forests, such as *Calycophyllum multiflorum* (Rivera *et al.* 2002), *Cedrela fissilis* (Santos & Takaki 2005), *Jacaratia corumbensis* (Frankie *et al.* 1974), *Myracrodruon urundeuva* and *Handroanthus impetiginosus* (Justiniano & Fredericksen 2000), demonstrating that vegetative patterns are strongly regulated by abiotic factors. Although several studies have shown strong relationships between climate variables and vegetative phenology, and little or no relation to reproductive phenology in tropical environments (Talora & Morellato 2000; Nunes *et al*. 2012), flowering and fruiting in the dry forests of the Pantanal plateau appear to be distinctly regulated by precipitation, temperature and day length. However, the responses of reproductive phenology differed among dispersal strategies, evidencing that, despite being sensitive to environmental variation, flowering and fruiting of the studied functional groups are under strong endogenous control.

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