



Reproductive phenology differs between evergreen and deciduous species in a Northeast Brazilian savanna

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ABSTRACT

Evergreen (EG) and deciduous (DEC) species exhibit distinct strategies to overcome dry periods and achieve adequate water status for reproduction and growth. Such particularities may result in distinct reproductive strategies between these groups. Thus, we evaluated the phenology of EG and DEC groups, comparing and differentiating their reproductive phenophases in an area of Brazilian savanna (*cerrado sensu stricto*), located in Mirador State Park, Maranhão State, by associating these patterns with leaf fall and flushing. Leaf fall, leaf flushing, flowering and fruiting data were monitored between April 2014 and March 2016 for 12 EG and 13 DEC species. To assess differences in flowering and fruiting patterns between EG and DEC, we compared phenological time, activity and intensity, and the duration of phenophases. We found earlier occurrence and longer duration of flowering for EG than for DEC; for fruiting, EG differed from DEC in activity throughout the year, with the intensity being greater for the EG group. These responses may reflect the distinct water-use strategies adopted by the EG and DEC groups, and confirm that differences in their ecophysiological strategies may exert an influence on their reproductive phenology.

Keywords: *cerrado*, flowering, fruiting, leaf fall, leaf flushing, leaf habit

Introduction

The classification of plant species as deciduous (DEC) and evergreen (EG) was developed as a manner to better understand ecophysiological strategies related to water acquisition, storage and transport to overcome the scarcity of this resource in ecosystems with a well-defined drought period (Eamus & Prior 2001). Many studies conducted in seasonal tropical ecosystems explored this functional classification to understand how marked seasonality directly influences vegetative and reproductive strategies (Franco *et al.* 2005; Ishida *et al.* 2006; Lenza & Klink 2006;

Rossatto 2013; Vico *et al.* 2015; Méndez-Alonzo *et al.* 2013; Tomlinson *et al.* 2014; Álvarez-Yépez *et al.* 2017).

According to such studies, evergreen species maintain high crown cover throughout the year (Fu *et al.* 2012), and possess leaves with a long life span and elevated shoot growth (Rossatto 2013). Physiological strategies of EG species include instantaneous decreased photosynthetic capacity, but higher photosynthetic capacity over the long term, coupled with more conservative water use (Eamus 1999; Franco *et al.* 2005). In contrast, deciduous species shed their leaves during the dry season, and exhibit strategies linked to reduced physiological activity and drought avoidance, which include higher stem hydraulic efficiency

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(Fu *et al.* 2012), elevated capacitance (Bucci *et al.* 2016) and the production of leaves with higher specific leaf area and elevated instantaneous photosynthetic capacity (Franco *et al.* 2005). Functional differences in leaves between DEC and EG species have been well documented over the past few decades (Takashima *et al.* 2004; Franco *et al.* 2005; Goldstein *et al.* 2008; Rossatto 2013; Vico *et al.* 2015; Tomlinson *et al.* 2014, Scalon *et al.* 2017), however, how distinct canopy maintenance strategies affect the occurrence and duration of aspects of reproduction have not been sufficiently explored.

Since evergreens maintain their canopy during drought periods through a series of strategies such as deep roots, decreases in leaf transpiration by stomatal control and low canopy cover, they are capable of assimilating carbon throughout the entire dry season, which in turn implies more available resources for flowering and fruit production during this adverse period (Jonasson 1989; Kloeppel *et al.* 2000). Deciduous species, in contrast, do not retain their canopy during the dry period because they are not capable of maintaining their leaves in the environment of high evaporative pressure during the dry season (Meinzer *et al.* 1999), even if being capable to reach soil layers with elevated moisture (Jackson *et al.* 1999; Goldstein *et al.* 2008). Deciduous species, however, rely on their lighter wood to store water in their trunks (Choat *et al.* 2005), such that they are able to slowly achieve adequate water balance and produce new leaves at the end of the dry period. Such differences between evergreen and deciduous plants may affect their reproductive strategies, since deciduous species achieve adequate water status latter in the dry season, in comparison with evergreen species (Hasselquist *et al.* 2010).

Phenological studies rely on investigations into the timing of recurrent life cycle events and their association with abiotic factors, such as precipitation, temperature and photoperiod, which act as strong selective pressures for phenological responses (Morellato *et al.* 2016; Mendoza *et al.* 2017; Lacerda *et al.* 2017). A series of approaches have been adopted in phenological studies, especially the use of functional groups with similar vegetative phenologies, to understand how life cycle events occur over time (Williams *et al.* 1999; Singh & Kushwaha 2006; Borges & Prado 2014). Studies using a functional group approach have reported that in tropical dry forests EG species exhibit longer flowering durations than DEC species, and that the two groups differ in the distribution and peaks of occurrence of reproductive events. It has also been reported that flowering periodicity might be associated with leaf loss and the time required for fruit development (Singh & Kushwaha 2006).

Brazilian savannas are subjected to strong climatic seasonality, which drives phenological events (Vilela *et al.* 2018) and allows the coexistence of species with different degrees of deciduousness. These species exhibit morphological traits and physiological mechanisms that allow their survival during the dry period (Franco *et al.* 2005; Souza *et al.* 2011; Scalon *et al.* 2017). Thus, considering the

fact that evergreen and deciduous species differ drastically in the way they conserve and use water resources during dry periods in savannas, we expected that phenological reproductive events would also differ between these two functional groups. Here we examine the reproductive phenology of EG and DEC species in a woody savanna in Northeast Brazil to determine whether flowering and fruiting behavior differ between DEC and EG in the following aspects: a) phenological time, b) activity and intensity of the phenophases and c) duration of phenophases. We hypothesized that the different water-use strategies of EG and DEC would affect the time, activity, intensity and duration of their flower and fruit production. Since EG species maintain their canopies during the drought period, they are expected to be able to produce flowers and fruits for longer periods during the dry season. In contrast, DEC species are expected to produce flowers and fruits for a short period in the late dry season, since their strategies imply a slow and gradual recovery of their water status throughout the entire dry season. These strategies are also expected to be associated with annual cycles of leaf fall and leaf production.

Materials and methods

Study area

The study was conducted between April 2014 and March 2016 in an area of Brazilian savanna (*cerrado sensu stricto*), located in Mirador State Park (06°37'55"S 45°52'38"W), a protected area in Maranhão State, Northeast Region of Brazil, covering 437,845 ha. The studied vegetation of the park has an average height of 3.9 m, with a density of 898.75 ind.ha⁻¹. *Qualea parviflora* Mart. is the plant species of this area with the highest importance value, and Fabaceae is the most represented family (data not published). According to Köppen's classification, the regional climate is Aw (Alvares *et al.* 2013), being tropical with distinct dry and rainy periods. Average annual rainfall is 1,200 mm (measured over a 30-year period); the monthly mean air temperature is 27 °C, with maximum and minimum monthly means of 33 °C and 22 °C, respectively (INMET 2016, Balsas station, n° 82.768). Elevation varies from 300 to 600 m, and the predominant soils in region are litolic neosols and yellow latosols. Monthly climatic data for the study period was obtained from the National Institute of Meteorology (INMET 2016, Balsas station, n° 82.768).

Species selection

Data were collected for twenty-five selected species (18 families) sampled in 20 randomly distributed plots (20 x 20 m, separated from each other by 100 m) in a typical savanna area of Mirador State Park. All individuals with



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a trunk circumference at ground level of ≥ 10 cm were sampled. The selected species were classified as evergreen (EG) or deciduous (DEC) (Tab. 1) based on information from the literature (Franco *et al.* 2005; Lenza & Klink 2006; Pirani *et al.* 2009; Rossatto 2013). Evergreen (EG) species were characterized by a high proportion of crown cover (generally close to or greater than 70%) during the entire year; deciduous (DEC) species were those that completely lose leaves during the dry period, typically for a period of more than four weeks (Franco *et al.* 2005).

Phenology

Between April 2014 and March 2016, the phenological behavior of all individuals of each species with a minimum of five individuals were monitored, and the phenophases of leaf fall, leaf flushing, flowering and fruiting for each individual visually estimated. Estimates were made according to percentage intensity as proposed by Fournier (1974), with the observed values distributed on a semi-qualitative scale comprising five categories: 0 to 4, in intervals of 25% (0: 0%;

Table 1. Studied woody species with distinct leaf phenologies (EG and DEC) in a savanna area of Mirador State Park, Northeast Brazil. N = number of sampled individuals, EG = evergreen, DEC = deciduous.

Family / Species	N	Leaf Phenology
Anacardiaceae		
<i>Anacardium occidentale</i> L.	15	EG
Apocynaceae		
<i>Himatanthus drasticus</i> (Mart.) Plumel	13	EG
<i>Hancornia speciosa</i> Gomes	5	DEC
Araliaceae		
<i>Schefflera burchellii</i> (Seem.) Frodin & Fiaschi	8	EG
Bignoniaceae		
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	5	DEC
Calophyllaceae		
<i>Kielmeyera speciosa</i> A.St.-Hil.	7	DEC
Caryocaraceae		
<i>Caryocar coriaceum</i> Wittm.	26	EG
Chrysobalanaceae		
<i>Hirtella ciliata</i> Mart. & Zucc.	27	EG
Connaraceae		
<i>Connarus suberosus</i> Planch.	51	EG
Ebenaceae		
<i>Diospyros hispida</i> A.DC.	12	DEC
Erythroxylaceae		
<i>Erythroxylum suberosum</i> A.St.-Hil.	16	DEC
Fabaceae		
<i>Leptolobium dasycarpum</i> Vogel	15	DEC
<i>Plathymenia reticulata</i> Benth.	13	DEC
<i>Stryphnodendron rotundifolium</i> Mart.	24	DEC
<i>Tachigali subvelutina</i> (Benth.) Oliveira-Filho	10	EG
Lythraceae		
<i>Lafoensia pacari</i> A.St.-Hil.	20	DEC
Melastomataceae		
<i>Mouriri elliptica</i> Mart.	9	EG
Myrtaceae		
<i>Myrcia splendens</i> (Sw.) DC.	5	EG
<i>Psidium myrsinites</i> DC.	13	DEC
Ochnaceae		
<i>Ouratea hexasperma</i> (A.St.-Hil.) Baill.	12	EG
Rubiaceae		
<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	17	DEC
Salicaceae		
<i>Casearia arborea</i> (Rich.) Urb.	10	EG
Vochysiaceae		
<i>Qualea grandiflora</i> Mart.	48	DEC
<i>Qualea parviflora</i> Mart.	41	DEC
<i>Salvertia convallariodora</i> A.St.-Hil.	12	EG



1: 1–25 %; 2: 26–50 %; 3: 51–75 % and 4: 76–100 %). The plants were generally considered to be under leaf fall when the crown was losing leaves; in leaf flushing when producing new leaves; in flowering when showing flower buds and/or open flowers; and in fruiting when immature and mature fruits were present.

To check for phenological differences between the EG and DEC groups in terms of flowering and fruiting patterns, we compared their phenological time, activity, intensity and duration of the reproductive phenophases. Phenological time was evaluated by onset date – mean angle in which each group manifested the phenophase for the first time – and peak date – mean angle in which each group showed the highest value for intensity – both estimated by population means (from individual estimates). Activity was represented by the monthly percentage of species manifesting the phenophases, and intensity by the monthly percentage of intensity, obtained as the mean intensity of the populations in each group, following the methodology described by Fournier (1974). Duration of phenophases was estimated for each group by population means, based on the average duration among individuals, and expressed in days.

In order to evaluate possible relationships between vegetative and reproductive events, we determined and compared leaf fall and leaf flushing for EG and DEC groups by evaluating their phenological time, activity and intensity, as described for reproductive phenophases. Leaf fall activity was not obtained because it occurred in all species throughout the year (even with low proportions in EG).

Statistical analysis

To test the occurrence of seasonal patterns in flowering and fruiting phenophases for EG and DEC groups, we used circular statistics (Morellato *et al.* 2000; 2010). Initially, months were converted into angles, in intervals of 30° (0° corresponding to January, until 330° corresponding to December). For these phenophases (flowering and fruiting) we calculated for each group (EG and DEC) their mean

angles, angular standard deviations and *r* vector lengths (considered as a measure of the degree of seasonality, ranging from zero to one) (Morellato *et al.* 2000; 2010), referring to onset and peak dates. To verify the occurrence of a seasonal pattern in the groups, the significance of angles were determined through the Rayleigh *z* test for circular distributions (Morellato *et al.* 2000; 2010). The circular analysis was carried out in the software ORIANA 4.0 (Kovach 2011). When a mean angle was significant, we performed the Watson-Williams test to verify whether the mean angles of the reproductive events differed between the functional groups (EG and DEC). The activity of reproductive phenophases in each functional group was compared using the G test (McDonald 2014). The intensity and duration of the reproductive phenophases were compared between the functional groups using the Mann-Whitney U test, considering that not all the samples conformed to the assumption of normality and variance homogeneity (Zar 2010).

Results

Leaf fall and flushing

The EG and DEC groups exhibit seasonality (Fig. 1A, B) for both vegetative parameters evaluated (Tab. 2). The peak leaf fall in DEC occurred in September, while for EG it was in August (Tab. 2.), although the differences were not significant ($F=2.21, p>0.05$). A greater intensity of leaf fall for DEC, than for EG, was confirmed ($U=164, p<0.05$).

Regarding leaf flushing, differences in mean onset ($F=14.03, p<0.01$) and mean peak dates ($F=6.79, p<0.05$), evidenced the earlier occurrence of this phenophase in the EG group, corresponding to August and September, respectively, while in DEC, both dates peaked in October. This phenophase exhibited greater seasonality in DEC (Tab. 2). Activity was distributed differently between groups ($G=118, p<0.01$), with greater percentages earlier for EG in relation to DEC.

Table 2. Circular statistics for flowering and fruiting onset and peak dates, for period between April 2014 and March 2016, for functional groups sampled in a Brazilian savanna area of Mirador State Park, Northeast Brazil. EG = evergreen; DEC = deciduous; LMV = length of mean vector (*r*). Mean vectors followed by the same letters were compared to each other. * indicates significant differences between the compared groups ($P<0.05$), according to Watson Williams test.

Variables	Phenofases													
	Leaf fall		Leaf flushing				Flowering				Fruiting			
	EG Peak(a)	DEC Peak(a)	EG Onset(b*)	EG Peak(c*)	DEC Onset(b*)	DEC Peak(c*)	EG Onset(d*)	EG Peak(e*)	DEC Onset(d*)	DEC Peak(e*)	EG Onset	EG Peak	DEC Onset	DEC Peak
Nº of observations	21	26	24	23	26	26	20	17	19	19	20	19	22	21
Mean Vector (μ)	223.36	240.86	229.57	260.55	280.25	298.60	225.52	234.77	292.55	292.38	250.77	279.61	177.04	201.39
Mean date	15 Aug	02 Sep	21 Aug	22 Sep	12 Oct	30 Oct	16 Aug	27 Aug	24 Oct	24 Oct	12 Sep	11 Oct	29 jun	24 jul
LMV (<i>r</i>)	0.77	0.96	0.59	0.52	0.94	0.96	0.5	0.52	0.59	0.63	0.51	0.52	0.27	0.31
Circular deviation	38.65	16.29	51.58	55.91	19.72	16.50	57.15	55.85	51.78	48.99	56.58	56.05	68.99	66.95
Rayleigh Test (Z)	15.52	23.94	8.49	6.59	23.01	23.89	6.06	6.34	3.49	4.02	6.04	6.25	0.83	1.1
Rayleigh Test (p)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.05	< 0.05	< 0.01	< 0.01	ns	ns



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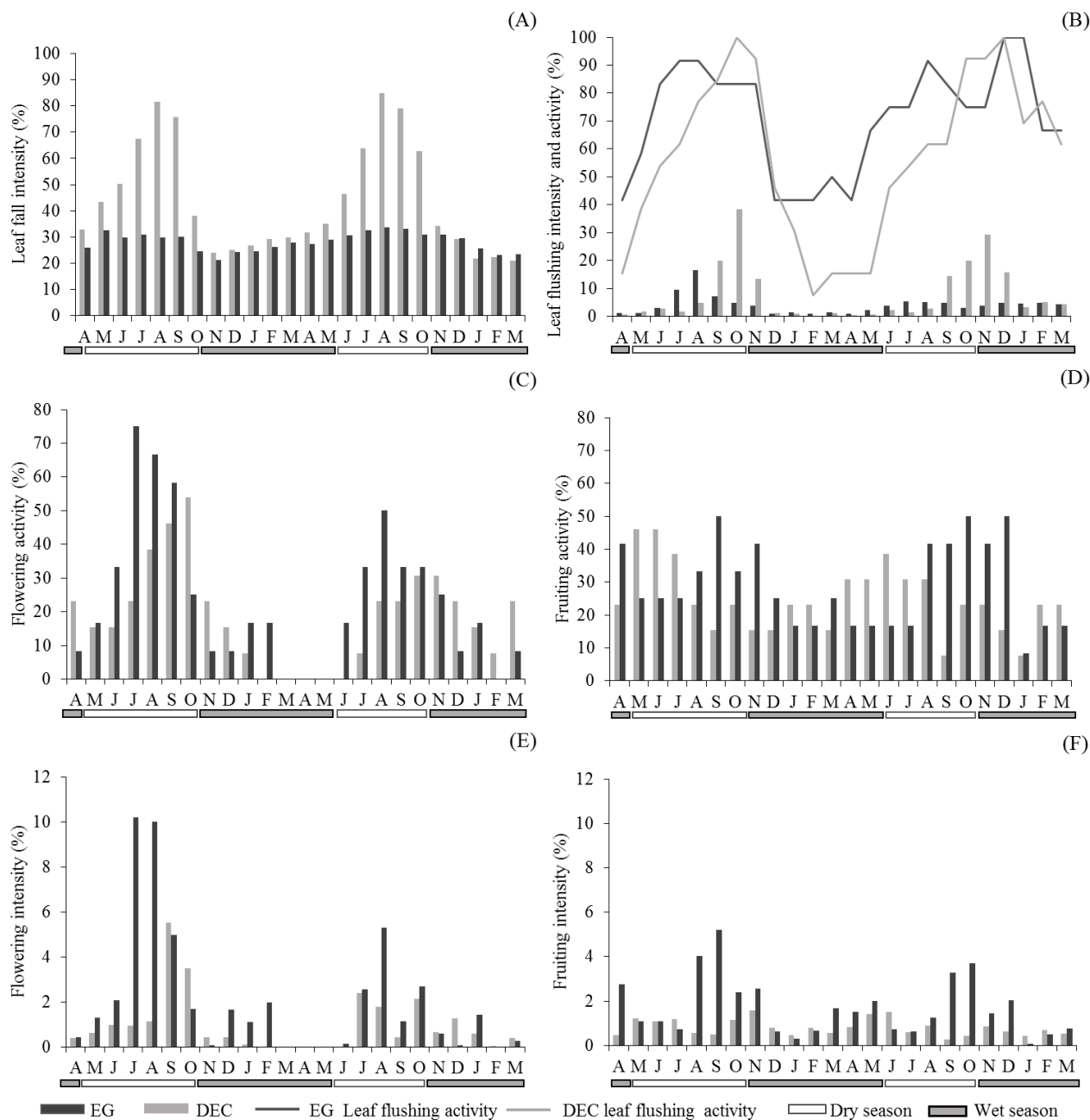


Figure 1. Average monthly distribution for evergreen (EG) and deciduous (DEC) groups of: **A.** intensity percentage of leaf fall; **B.** activity and intensity percentages of leaf flushing; **C- D.** flowering and fruiting activities; **E-F.** flowering and fruiting intensities. Mirador State Park, Northeast Brazil. Letters represent the initials of the months of the year between April 2014 and March 2016. Bars below the x-axis represent the dry and wet months of the study period.

Flowering

The EG and DEC groups showed seasonal patterns for flowering (Tab. 2), with concentrated mean dates appearing during the dry season. The mean onset and mean peak dates also differed between the functional groups ($F=6.7$, $p<0.05$; $F=4.6$, $p<0.05$). In the EG group, the mean angles for onset and peak corresponded to the month of August, in the same month of leaf fall and leaf flushing peaks (Tab. 2).

In DEC, the mean date of flowering was concentrated in October (Tab. 2), while the leaf flushing dates in this group occurred and almost two months after the leaf fall peak (Tab. 2). Flowering activity also differed between EG and DEC throughout the year ($G=164.34$, $p<0.01$) (Fig. 1C). Both groups showed higher percentages of activity between July and December, corresponding to the dry period and early in the rainy season. In general, the percentage values for flowering were higher and appeared earlier in EG, between

July and August; in DEC, an evident increase in activity was found in August, extending to December. For both groups, flowering occurred when leaf fall began to decrease and concomitant with the leaf-flushing period or just after (Fig. 1A-C). Exceptions were found for the deciduous *Hancornia speciosa* and *Tabebuia aurea*, whose flowering occurred during the period of leaf senescence, prior to total deciduousness. Other exceptions included the deciduous *Qualea grandiflora* and the evergreen *Schefflera burchellii*, whose flowering occurred with leaves already fully expanded.

We did not find significant differences between the groups in flowering intensity ($U=218, p>0.05$), although greater values were observed for EG (Fig. 1E). Flowering intensity was more variable than flowering activity, due to the influence of variation in percentage intensity at the species level (Fig. 1C-E). For example, among the EG species, *Casearia arborea* and *S. burchellii* had higher flowering intensity between December and February, which increased the total intensity for this group. As for the DEC, increased intensity was observed in July due to the flowering of *T. aurea*.

The EG and DEC groups differed in the duration of their flowering ($U=27, p < 0.05$), with a median of 48 days for EG, and 39 days for DEC.

Fruiting

Significant seasonality was observed for the mean onset and mean peak dates of fruiting only for the EG group (Tab. 2), thus EG and DEC were not compared by the Watson Williams test. Fruiting activity differed between EG and DEC ($G=141.64, p<0.01$) and was irregularly distributed in comparison to flowering for both groups. This was more evident in the DEC, although this group had higher percentages between May and August, which is the end of the rainy period and part of the dry period. In general, in the EG group fruiting increased after the initial period of leaf flushing (Tab. 2), when the canopy was already partially or completely recomposed (Fig. 1B, D). In DEC, fruiting activity increased when leaf fall began, but before full deciduousness (Fig. 1A, D). Fruiting occurred during the leaf flushing period in the species *Diospyros hispida* and *Erythroxylum suberosum*, and with fully expanded leaves in *Tocoyena formosa*, during the rainy season for all these species. In EG, fruiting activity had higher percentages from September to December, which corresponds to late in the dry season and part of the rainy season, after a high percentage of leaf flushing (Fig. 1D).

The fruiting intensity was greater in EG than in DEC ($U=164, p<0.01$), and exhibited an additional peak in EG (between the months of March and May) different from fruiting activity (Fig. 1F), which corresponds to the high fruiting intensity of the species *Mouriri elliptica* and *S. burchellii*. Variation was greater in DEC than in EG, with a distinct response in relation to activity. In this group (DEC),

for example, a high percentage of fruiting by *E. suberosum* (in the first year) increased the intensity in October and December (Fig. 1F).

Fruiting duration did not differ significantly between the functional groups ($U=47, p > 0.05$). EG had a median duration of 57 days, while DEC had 51 days.

Discussion

Our predictions concerning differences in reproductive phenology between EG and DEC plants were confirmed. We found clear differences regarding the time, activity and duration for both flowering and fruiting (activity and intensity) between the two groups of studied savanna species. In addition, we observed differences in the time of vegetative phenology associated with reproductive events. These results provide evidence that the distinct ecophysiological strategies adopted by EG and DEC may exert significant influence on their phenological reproductive behavior.

We found seasonality in flowering for both functional groups, which occurred from middle to late in the dry period for EG, and late in the dry season to early in the rainy season for DEC. These results, found for the majority of studied species, were similar to those reported for environments with marked water seasonality, with flowering occurring in the dry season (Williams *et al.* 1999; Singh & Kushwaha 2006; Pirani *et al.* 2009), but especially during the transition between dry and rainy periods (Lenza & Klink 2006; Selwyn & Parthasarathy 2006; Silverio & Lenza 2010). In the present study, the early occurrence of flowering onset and peak dates, associated with differences in flowering activity, converge in the same direction, indicating that flowering in EG occurs earlier. This discrepancy between the groups occurred in clear association with the period of new leaf production, usually preceding or concomitant with it. It is possible that this fact is intrinsically associated with the annual cycles of leaf senescence and production, indicating different strategies regarding the use of resources, both internal and available in the environment (Fu *et al.* 2012; Lima *et al.* 2012).

The significant increase in flowering activity by DEC species late in the dry season and early in the rainy season indicates that this event starts under severe seasonal water restriction in the environment, but not for the plants, which have mechanisms for tissue rehydration (Holbrook 1995; Goldstein *et al.* 1998; Scholz *et al.* 2007). During the leafless period, the gradual restoration of water levels is expected in DEC species, which is associated with their efficient hydraulic characteristics (Fu *et al.* 2012), especially the use of water stored in the trunk (Borchert 1994). This mechanism provides adequate conditions for DEC plants to gradually increase their capacity for water retention, until late in the dry season (Borchert *et al.* 2004; Franco *et al.* 2005), when flowering increases. Thus, a consistent



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pattern is observed, similar to the schedule for species of the drought-deciduous species group, which may respond to changes in temperature or photoperiod for leaf production (Vico *et al.* 2015). Another possibility is that flowering starts during the end of the dry season because DEC seeds need to germinate promptly when water and nutrients are available in the rainy season (Scholes & Walker 2004; Nord & Lynch 2009). In this way, the time required for fruiting and seed dispersal can determine the time of occurrence of this phenomenon (Singh & Kushwaha 2006). These events are interconnected in time to adjust plant fitness in seasonally hydric conditions (Kimball *et al.* 2012).

For most DEC species, flowering occurred partially or completely during the leaf-flushing period, ranging from late in the dry season to early in the rainy season. For the species *Lafoensia pacari*, *H. speciosa* and *T. aurea*, flowering occurred earlier than in other species, during the first half of the dry period and concomitantly with senescence and leaf fall, while for *Q. grandiflora*, flowering occurred after that of the other species, in the rainy season and with full crown. These responses, which diverge from the general pattern, led to low synchrony (lower vector length) among onset and peak dates. Thus, although a general response was found for DEC species, alternative patterns can emerge and may reflect different strategies of water absorption and storage, and resource allocation, in this group (Lima *et al.* 2012; Wolfe & Kursar 2015).

In EG, both the occurrence of onset and peak dates during drought and differences in activity percentages represented particularities that are clearly associated with the foliar habit of this group. Flowering in the mid-dry period reinforces the presence of strategies related to drought tolerance, supported by known physiological mechanisms that minimize water loss and maintain photosynthetic activity and sufficient carbon gain, thus allowing the maintenance of production activities during the dry season (Eamus & Prior 2001). In this group, leaf exchange and flowering occurred simultaneously and earlier in relation to DEC, indicating the reestablishment of growth, possibly due to the mobilization of water and nutrients by plants. Thus, internal alterations compensate for water limitations of the environment, such as water storage, adjustment of tissue osmotic potential and reduction of leaf transpiration – by stomatal conductance – which thereby favors early flowering (Meinzer *et al.* 1999). Additionally, these conditions result in advantages for flowering, such as the reduction of damage to flowers by rainfall, herbivory and increased activity of pollinating agents, mainly represented by bees (Janzen 1980; Schaik *et al.* 1993).

Regarding flowering duration, two situations seem to explain the differences found between the groups: although in both groups flowering generally occurs during the leaf flushing period, in the deciduous group it generally coincides with a short and intense period of leaf flushing. This relationship may correspond to high mobilization of reserves

to be used in the development of both leaves and flowers, which may decrease the flowering period in this group. In EG, the longer flowering duration associated with gradual leaf flushing may be related to drought tolerance strategies, which allow for a longer investment in production activities (*e.g.* leaves and flowers). Thus, we assume that flowering duration is linked to differences in resources use between EG and DEC (Tomlinson *et al.* 2013). A similar response was found by Borges & Prado (2014) in Brazilian savannas, who associated it with the availability of resources from photosynthesis and branch inclination, which may favor the protection of reproductive structures by the presence of permanent leaves.

Regarding fruiting, the fruit development phases of both groups extended into the dry and rainy periods. Although only the EG species showed significant seasonality, differences related to fruiting activity between functional groups indicates a possible association with the different requirements for fruit development of each group, mesocarp type (fleshy and dry), and dispersal and seed germination strategies. The fruiting activity in EG increased rapidly after flowering, late in the dry season and early in the rainy season, indicating an efficient allocation of resources for fruit production. It is possible that this is related to conditions that facilitate the maintenance of fleshy fruits and to a larger number of dispersal agents during the period of greater humidity. Moreover, this behavior may allow seeds to germinate and establish during the wet season (Venable & Brown 1988; Fenner 1985). However, there were three exceptions in this group: the species *Salvertia convallariodora* and *Himatanthus drasticus* (both of which have dry fruits), whose fruiting was recorded exclusively during the dry period, and *S. burchellii*, whose fruiting occurred in the transition from the rainy to the dry season. In these species, features related to seed characteristics and germination requirements may possess particularities that complement the explanations of these findings (Vieira *et al.* 2008; Bewley & Black 2012).

In DEC species, the peak of fruiting activity late in the rainy season and early in the dry season, may reflect a requirement for a supply of water for fruit development during almost the entire rainy season and dispersion facilitated by the conditions in the following dry season, when there is less crown coverage by leaves, thus facilitating dispersion. The production of orthodox seeds with longer longevity is common among DEC species, which may explain fruiting early in the dry season (Figueiredo 2008). For other species in this group that possess fleshy fruits, fruiting during the rainy season may be associated with different desiccation tolerances of seeds or to the occurrence of dormancy, which can complement the interpretation of the data (Tweddle *et al.* 2003; Vieira *et al.* 2008). The greater fruiting intensity percentage for EG species, in relation to DEC species, is supposedly associated with mechanisms that favor efficient pollination in this group,



however, investigations that address more specific aspects are necessary and may provide new insights into this. Aspects related to investments in fruit production after the maximum period of leaf production may contribute to further understanding, since the allocation of photosynthesis products, which is more efficient in new leaves, can be harnessed for the production of a large number of fruits.

Differences in flowering and fruiting between evergreen and deciduous species support the different functions related to this classification. We showed that being deciduous or evergreen implies certain specific characteristics related to the time of occurrence (onset and peak dates), activity, duration and intensity of reproductive events, which are intrinsically coupled with patterns of leaf fall and flushing.

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References

- Alvares CA, Stape JL, Sentelhas PC, Moraes G, Leonardo J, Sparovek G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711-728.
- Álvarez-Yépez JC, Búrquez A, Martínez-Yrizar A, Teece M, Yépez EA, Dovciak M. 2017. Resource partitioning by evergreen and deciduous species in a tropical dry forest. *Oecologia* 183: 607-618.
- APG – Angiosperm Phylogeny Group IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1-20.
- Bewley JD, Black M. 2012. Physiology and biochemistry of seeds in relation to germination: Vol II - Viability, dormancy and environmental control. Heidelberg, Springer Science & Business Media.
- Borchert R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437-1449.
- Borchert R, Meyer SA, Felger RS, Porter-Bolland L. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409-425.
- Borges MP, Prado CHB. 2014. Relationships between leaf deciduousness and flowering traits of woody species in the Brazilian neotropical savanna. *Flora* 209: 73-80.
- Bucci SJ, Goldstein G, Scholz FG, Meinzer FC. 2016. Physiological significance of hydraulic segmentation, nocturnal transpiration and capacitance in tropical trees: Paradigms revisited. In: Goldstein G, Santiago L. (eds.) *Tropical tree physiology*. Cham, Springer International Publishing. p. 205-225.
- Choat B, Ball MC, Lully JG, Holtum JA. 2005. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees* 19: 305-311.
- Eamus D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology & Evolution* 14: 11-16.
- Eamus D, Prior L. 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Advances in Ecological Research* 32: 113-197.
- Fenner MW. 1985. *Seed ecology*. London, Chapman and Hall.
- Figueiredo PS. 2008. Fenologia e estratégias reprodutivas das espécies arbóreas em uma área marginal de cerrado, na transição para o semi-árido no nordeste do Maranhão, Brasil. *Revista Trópica* 2: 8-21.
- Fournier LA. 1974. Un método cuantitativo para la medición de características fenológicas en árboles. *Turrialba* 24: 422-423.
- Franco AC, Bustamante M, Caldas LS, et al. 2005. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees* 19: 326-335.
- Fu PL, Jiang YJ, Wang AY, et al. 2012. Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Annals of Botany* 110: 189-199.
- Goldstein G, Andrade JL, Meinzer FC, et al. 1998. Stem water storage and diurnal patterns of water use in tropical Forest canopy trees. *Plant Cell and Environment* 21: 397-406.
- Goldstein G, Meinzer FC, Bucci SJ, Scholz FG, Franco AC, Hoffmann WA. 2008. Water economy of Neotropical savanna trees: six paradigms revisited. *Tree Physiology* 28: 395-404.
- Hasselquist NJ, Allen MF, Santiago LS. 2010. Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* 164: 881-890.
- Holbrook NM. 1995. Stem water storage. In: Gartner BL. (ed.) *Plant stems: physiology and functional morphology*. San Diego, Academic Press. p. 151-174.
- INMET – Instituto Nacional de Meteorologia. 2016. Banco de dados meteorológicos para ensino e Pesquisa, BDMEP. <http://www.inmet.gov.br/portal>. 02 Apr. 2016.
- Ishida A, Diloksumpun S, Ladpala P, et al. 2006. Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. *Tree Physiology* 26: 643-656.
- Jackson PC, Meinzer FC, Bustamante M, et al. 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree physiology* 19: 717-724.
- Janzen, DH. 1980. *Ecologia vegetal nos trópicos*. São Paulo, EPU.
- Jonasson S. 1989. Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. *Oikos* 56: 121-131.
- Kimball S, Gremer JR, Angert AL, Huxman TE, Venable DL. 2012. Fitness and physiology in a variable environment. *Oecologia* 169: 319-329.
- Kloeppel BD, Gower ST, Vogel JG, Reich PB. 2000. Leaf-level resource use for evergreen and deciduous conifers along a resource availability gradient. *Functional Ecology* 14: 281-292.
- Kovach WL. 2011. *Oriana—circular statistics for windows*. Ver. 4. Pentraeth, Kovach Computing Services.
- Lacerda DMA, Barros JBA, Almeida Jr. EB, Rossatto DR. 2017. Do conspecific populations exhibit divergent phenological patterns? A study case of widespread savanna species. *Flora* 236-237: 100-106.
- Lenza E, Klink CA. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Revista Brasileira de Botânica* 29: 627-638.
- Lima ALA, Sampaio EVDSB, Castro CC, Rodal MJN, Antonino ACD, Melo AL. 2012. Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? *Trees* 26: 1605-1616.
- McDonald JH. 2014. *Handbook of Biological Statistics*. 3rd. edn. Baltimore, Sparky House Publishing.
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavellier J, Wright SJ. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121: 293-301.
- Méndez-Alonzo R, Pineda-García F, Paz H, Rosell JA, Olson ME. 2013. Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. *Trees* 27: 745-754.
- Mendoza I, Peres CA, Morellato LPC. 2017. Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change* 148: 227-241.
- Morellato LPC, Alberti LF, Hudson IL. 2010. Applications of circular statistics in plant phenology: a case studies approach. In: Keatley M, Hudson IL. (eds.) *Phenological research: methods for environmental and climate change analysis*. New York, Springer. p. 357-371.



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- Morellato LPC, Alberton B, Alvarado ST, *et al.* 2016. Linking plant phenology to conservation biology. *Biological Conservation* 195: 60-72.
- Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* 32: 811-823.
- Nord EA, Lynch JP. 2009. Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany* 60: 1927-1937.
- Pirani FR, Sanchez M, Pedroni F. 2009. Fenologia de uma comunidade arbórea em cerrado sentido restrito, Barra do Garças, MT, Brasil. *Acta Botanica Brasilica* 23: 1096-1109.
- Rossatto DR. 2013. Seasonal patterns of leaf production in co-occurring trees with contrasting leaf phenology: time and quantitative divergences. *Plant Species Biology* 28: 138-145.
- Scalon MC, Haridasan M, Franco AC. 2017. Influence of long-term nutrient manipulation on specific leaf area and leaf nutrient concentrations in savanna woody species of contrasting leaf phenologies. *Plant and Soil* 421: 233-244.
- Schaik CP, Terborgh JW, Wright S.J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353-377.
- Scholes RJ, Walker BH. 2004. *An African savanna: synthesis of the Nylsvley study*. Cambridge, Cambridge University Press.
- Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Miralles-Wilhelm F. 2007. Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant, Cell & Environment* 30: 236-248.
- Selwyn MA, Parthasarathy N. 2006. Reproductive traits and phenology of plants in tropical dry evergreen forest on the Coromandel coast of India. *Biodiversity & Conservation* 15: 3207-3234.
- Silvério DV, Lenza E. 2010. Fenologia de espécies lenhosas em um cerrado típico no Parque Municipal do Bacaba, Nova Xavantina, Mato Grosso, Brasil. *Biota Neotropica* 10: 205-216.
- Singh KP, Kushwaha CP. 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Annals of Botany* 97: 265-276.
- Souza JP, Prado CH, Albino AL, Damascos MA, Souza GM. 2011. Network analysis of tree crowns distinguishes functional groups of Cerrado species. *Plant ecology* 212: 11-19.
- Takashima T, Hikosaka K, Hirose T. 2004. Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant, Cell & Environment* 27: 1047-1054.
- Tomlinson KW, Poorter L, Bongers F, Borghetti F, Jacobs L, Langevelde E. 2014. Relative growth rate variation of evergreen and deciduous savanna tree species is driven by different traits. *Annals of Botany* 114: 315-324.
- Tomlinson KW, Poorter L, Sterck FJ, *et al.* 2013. Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *Journal of Ecology* 101: 430-440.
- Tweddle JC, Dickie JB, Baskin CC, Baskin JM. 2003. Ecological aspects of seed desiccation sensitivity. *Journal of Ecology* 91: 294-304.
- Venable DL, Brown JS. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist* 131: 360-384.
- Vico G, Thompson SE, Manzoni S, *et al.* 2015. Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. *Ecohydrology* 8: 660-681.
- Vieira DLM, Lima VV, Sevilha AC, Scariot A. 2008. Consequences of dry-season seed dispersal on seedling establishment of dry forest trees: Should we store seeds until the rains? *Forest Ecology and Management* 256: 471-481.
- Vilela AA, Claro VT, Torezan-Silingardi HM, Del-Claro K. 2018. Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod-Plant Interactions*. 12: 215-227.
- Williams RJ, Myers BA, Eamus D, Duff GA. 1999. Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica* 31: 626-636.
- Wolfe BT, Kursar TA. 2015. Diverse patterns of stored water use among saplings in seasonally dry tropical forests. *Oecologia* 179: 925-936.
- Zar JH. 2010. *Biostatistical analysis*. New Jersey, Prentice-Hall.

