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Original Paper

Phenological dynamics of *Croton heliotropiifolius* populations in a savanna/caatinga gradient, Chapada Diamantina, Brazil

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Abstract

The relationship between phenology and environmental factors is critical to understanding population dynamics in environmental gradients. We evaluated phenological variations in *Croton heliotropiifolius* Kunth in sites with contrasting water resource availability in caatinga, cerrado/caatinga transition, and cerrado in the Chapada Diamantina, Brazil. The phenophases of 81 individuals (n = 27 individuals/area) were recorded monthly for 12 months. Multiple regression, Spearman correlation, circular statistics, Shannon-Wiener diversity, and Morisita-Horn indices were used to test relationships between phenophases and abiotic factors, phenological seasonality, diversity, and similarities between the three populations. The vegetative behaviors in the study sites were distinct in terms of their intensity, seasonality, and synchrony; but reproductive phenophases maintained similar characteristics. Phenological events were positively related to rainfall and soil water availability. *C. heliotropiifolius* populations exhibited high levels of vegetative phenological diversity, except in the caatinga during the dry season. Reproductive phenological diversity varied along the studied period in the three sites, with higher reproductive than vegetative similarities among populations. Differences in soil types and rainfall volumes in the dry season, even at small distances, therefore make the savanna/caatinga gradient a suitable model for investigating phenological responses related to plant eco-hydrological strategies in seasonally tropical dry ecosystems.

Key words: phenological diversity, rainfall, seasonally dry tropical ecosystems, soil water availability, synchrony.

Resumo

A relação entre fenologia e fatores ambientais é chave para compreender a dinâmica de populações em gradientes ambientais. Foram avaliadas variações fenológicas de *Croton heliotropiifolius* Kunth em sítios, com disponibilidade hídrica contrastante, de caatinga, transição cerrado/caatinga e cerrado, na Chapada Diamantina, Brasil. Fenofases de 81 indivíduos (n = 27 indivíduos/área) foram registradas mensalmente por 12 meses. Regressão múltipla, correlação de Spearman, estatística circular, índice de diversidade de Shannon-Wiener e índice de Morisita-Horn foram usados para testar relações entre fenofases e fatores abióticos, sazonalidade fenológica, diversidade e similaridade entre as populações. As fenofases vegetativas foram distintas em intensidade, sazonalidade e sincronia; enquanto as fenofases reprodutivas mantiveram-se similares. Os eventos fenológicos foram relacionados positivamente à precipitação e disponibilidade de água no solo. As populações de *C. heliotropiifolius* exibiram altos níveis de diversidade fenológica vegetativa, exceto na caatinga durante a seca. A diversidade fenológica reprodutiva variou no período estudado nos três sítios. Houve maior semelhança reprodutiva entre as populações, do que vegetativa. Diferenças nos tipos de solo e volumes de chuva na estação seca, mesmo em pequenas distâncias, tornam o gradiente cerrado/caatinga um modelo adequado para investigar respostas fenológicas relacionadas a estratégias eco-hidrológicas de plantas em ecossistemas sazonalmente secos tropicais.

Palavras-chave: diversidade fenológica, precipitação, ecossistemas tropicais sazonalmente secos, disponibilidade de água no solo, sincronia.

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Introduction

Phenological studies examine cyclical biological events and their relationships to abiotic and biotic factors (Lieth 1974). In tropical areas, phenological response of plants has been more frequently associated with variation in rainfall (Borchert 1998; Miranda *et al.* 2011; Dalmolin *et al.* 2015; Vico *et al.* 2015; Lacerda *et al*. 2018; Menezes *et al.* 2018; Vilela *et al.* 2018). The role of photoperiod in inducing bud breaking and flowering in tropical plants has been found to be important in environments where water balances remain positive throughout the year (Borchert & Rivera 2001; Borchert *et al.* 2005; Calle *et al.* 2010; Souza & Funch 2017). Temperature changes have been regarded as a less important phenological trigger in tropical plants (Morellato *et al.* 2000; 2013).

The importance of the availability of water to plants (reflecting rainfall and soil characteristics) has been emphasized as linked to environmental heterogeneity (Borchert *et al.* 2002). Phenological variations have been studied in several tropical species along their distribution ranges considering differences in rainfall, irradiance, and soil properties (Seghieri & Simier 2002; Goulart *et al.* 2005; Lemos Filho *et al.* 2008; Cardoso *et al.* 2012; Capuzzo *et al.* 2012; Toledo *et al*. 2012; Rossatto 2013; Moraes *et al.* 2017; Neves *et al.* 2017). Those studies were directed to better understanding the influences of environmental factors on the phenological behaviors of populations associated with different types of forests, and the factors that determine species distributions.

The selective pressures imposed by environmental gradients on water availability are reflected in phenological patterns and can be analyzed by monitoring species distributed in different habitats (Capuzzo *et al*. 2012; Toledo *et al*. 2012; Moraes *et al.* 2017). Widely distributed species can demonstrate intra-specific variations in their functional traits even at very short distances and can occupy a variety of environments due to their high adaptability (Rossato *et al.* 2013; Mitchell & Bakker 2014; Moraes *et al.* 2017). Associations between cerrado (Neotropical savanna) and caatinga (seasonally dry tropical forest-SDTF) vegetations along environmental gradients of water availability have been described (Pennington *et al*. 2009; Neves *et al*. 2016; 2017). Savanna vegetation is mostly found on deep soils in regions subject to frequent fires and climatic seasonality. Those conditions drive phenological events and allow the coexistence of species having differing degrees of deciduousness and distinct episodes of flowering and fruiting during the year (Franco *et al.* 2005; Souza *et al*. 2011; Lacerda *et al.* 2017; Neves *et al.* 2017; Scalon *et al*. 2017; Camargo *et al.* 2018; Lacerda *et al*. 2018; Vilela *et al*. 2018). Caatinga vegetation is exposed to long and unpredictable dry periods and grows on several types of soil that are usually much shallow than those found in savanna areas (Pennington *et al.* 2009; Coelho *et al*. 2013; Sánchez-Azofeifa *et al.* 2013). Rainfall plays a fundamental role in determining the frequency and duration of phenological events in the caatinga, with budding, flowering, and fruiting almost fully restricted to the rainy season (Lima & Rodal 2010; Lima *et al.* 2012; Neves *et al*. 2017).

The environmental heterogeneity observed in the Chapada Diamantina mountains, in northeastern Brazil, is reflected in its predominant mosaic of campo rupestre, savanna, caatinga, and seasonal forest vegetations (Funch *et al.* 2009), with adjacent patches of savanna and caatinga experiencing a semiarid and highly seasonal climate and growing on different soil types with distinct water availabilities (Neves *et al.* 2016; 2017). Neves *et al.* (2017) reported variations in phenological responses at the community level in a savanna/caatinga gradient that were associated with differences in the physical properties of the soil and with rainfall during the dry season – resulting in the selection of species with distinct water-use strategies and demonstrating continuous flowering patterns in savanna vegetation, while demonstrating seasonal flowering patterns associated with rainfall in transition and SDTF areas.

The genus *Croton* (Euphorbiaceae) comprises plants with heterogeneous habits, and such as trees, shrubs, subshrubs, herbs, and vines (Radulovic *et al*. 2006) and/or especially diverse in Brazil (350 species) and represented in a wide variety of environments and vegetation types (Lima & Pirani 2008; Oliveira *et al*. 2016). Neves *et al.* (2016, 2017) determine that one of the few species that occurs continuously along the savanna/caatinga gradient in the Chapada Diamantina is *Croton heliotropiifolius* Kunth (Euphorbiaceae), a species widely distributed in northeastern Brazil (Silva *et al.* 2010; Flora do Brasil 2020).

The continuous distribution of *C. heliotropiifolius* in that savanna/caatinga gradient presents an excellent opportunity to investigate intraspecific variations of vegetative and reproductive phenophases in response to environmental variations. We sought to examine the phenological responses (seasonality, synchrony, and intensity) of *C. heliotropiifolius* populations in relation to environmental variations (rainfall, and soil moisture) along that savanna/caatinga gradient, hypothesizing that seasonality and phenological synchrony would be higher in the caatinga and savanna/caatinga transition sites than in the savanna, and would include adjustments in the phases of leaf and floral bud production during the rainy season. The savanna, on the other hand, would be expected to exhibit more continuous foliar and reproductive rhythms, with greater asynchrony of its phenophases. We therefore predicted greater similarity of the reproductive phenological events of *C. heliotropiifolius* individuals in the caatinga and transition areas, but greater diversity of the phenological responses of individuals in the savanna site.

Material and Methods

Study species and site

Chapada Diamantina is located in the northern region of the Espinhaço Range, which covers an area of 50,610 km^2, and comprises a mosaic of savanna, arboreal caatinga, forest and, especially, campo rupestre vegetation (Funch *et al.* 2009). Large rock outcrops and litholic neosols (shallow, stony, low fertility soils) occur on massifs and tall mountains, while latosols (deep, well-drained, acidic, low fertility soils) occur on plateaus (Juncá *et al.* 2005). The region has a tropical climate (type Aw based on the Köppen system; Alvares *et al.* 2013) characterized by rainy summers and dry winters, with a rainy season from November to April, and a dry season from June to October (Funch *et al.* 2002). The historical averages of temperature and rainfall were 24ºC and 100 mm respectively, varying between 25º C and 55 mm during the dry season, and 22º C and 155 mm during the rainy season (Instituto Nacional de Meteorologia - INMET).

The study was conducted in two contiguous vegetation types west of the Chapada Diamantina National Park (savanna [12º 26’ 7.6” S, 41º 31’ 3.6” W; 884 m a.s.l.] and caatinga [12º 27’ 8.74” S, 41º 35’ 49.80” W; 697 m a.s.l]), as well as in the area of savanna/caatinga transition area between them (12º 26’ 33.6” S, 41º32’ 1” W; 736 m a.s.l) (Fig. 1). The savanna vegetation is composed of a continuous herbaceous layer and shrub-arboreal species (5 to 50% percent tree cover) from 2 to 8 m tall. The transition and caatinga areas lack a continuous herbaceous layer but have a discontinuous canopy of shrubs and trees that can reach 10 m tall. The vegetation in the transition area is physiognomically similar to the caatinga, with floristic elements of the savanna. The soils in the savanna are sandy, while those in the transition and caatinga areas are sandy-clayey and acidic. The soils in the three areas are dystrophic (alkaline saturation < 50%), acidic (pH < 5), non-aluminous (Al < 1.3 cmol/dm^3, except in the transition area) and have low cation exchange capacities (CEC < 13) with high H^+ and Al^{+3} loads (Neves *et al.* 2016) (Fig. 1).

Croton heliotropiifolius is a subshrub or shrub up to 2.5 m tall, monoecious, with unisexual flowers gathered in inflorescences, the female flowers at the base and the male flowers at the apex (Carneiro-Torres 2009). *C. heliotropiifolius* is widely distributed in the study region and occurs widely in northeastern Brazil in caatinga vegetation, although it also occurs in montane forest, restinga, and savanna vegetation (Carneiro-Torres 2009; Silva *et al.* 2009; Silva *et al.* 2010; Flora do Brasil 2020). The marked individuals of *C. heliotropiifolius* were subshrubs or shrubs with heights varying from 0.46 m to 1.75 m in the savanna, 0.43 m to 1.46 m in the transition area, and 0.56 m to 1.26 m in the caatinga. The distance between marked plants varied from two to ten meters.

Environmental data

The historical data for average annual rainfall and temperature are from 1965 to 2016 and were obtained from the Instituto Nacional de Meteorological (INMET) (Fig. 2a). The photoperiod data was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/docs/RS_OneYear.php>) (Fig. 2b). The rainfall data was obtained from rain gauges installed in each environment (Fig. 2c). Temperatures were measured using a sensor (WatchDog, model 1400, Spectrum Technologies) located approximately 1 km from the caatinga area, 8 km from the transition area, and 9.5 km from the savanna area.

Soil moisture was measured using the gravimetric method, based on soil samples collected at depths of 0 to 20 and 21 to 40 cm (Fig. 2c). Six samples were collected from each habitat, totaling 18 samples per month, for 12 months. To avoid the loss of water, the samples were sealed in aluminum

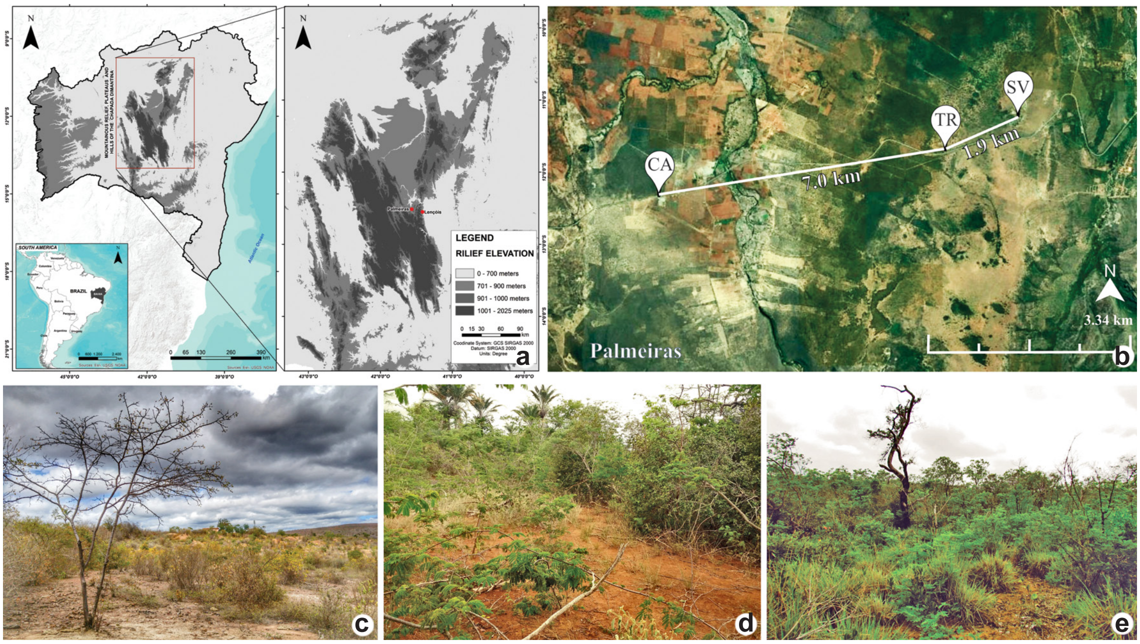

Figure 1 – Location of the forest study sites in the Chapada Diamantina mountains, Brazil. a. Chapada Diamantina mountains; b. Google Earth image, indicating the distances between the studied forests: Caatinga (CA), Savanna-caatinga transition (TR), Savanna (SV); c. Caatinga; d. Savanna-caatinga transition; e. Savanna.

cans, which were numbered and of known weight (70 g), until the samples were weighed to obtain their wet weight. To obtain their dry weights, the samples were dried in an oven at 105º C (Embrapa 2011). That data was used to calculate the monthly gravimetric water contents of the soil: gravimetric water content (Gw) = (wet weight – dry weight) / (dry weight) × 100, data in grams (g). Monthly rainfall and soil moisture in the areas, during the study period, are presented in Figure 2c.

Phenology

Phenological observations were made on a total of 81 marked adult individuals in the savanna (n=27), savanna/caatinga transition (n=27), and caatinga (n=27), at monthly intervals from July 2017 to June 2018. The vegetative phenophases observed were leaf flushing (LF), young leaves (YL), and leaf fall (LFL); and the reproductive phenophases were male buds (MB), female buds (FB), male flowers (MF), female flowers (FF), immature fruits (IFT), and mature fruits (MFT). The intensities of the phases were estimated using a semi-quantitative scale with five categories (0 to 4, at intervals of 25%), as proposed by Fournier (1974). The intensity of each phase, expressed as a percentage based on the five categories (San Martin-Gajardo & Morellato 2003), was converted into linear graphs. The intraspecific synchrony of phenological events was evaluated for each population according to Bencke & Morellato (2002), where the percentage of individuals of a population exhibiting each phenophase in a time interval is determined using the following classification: asynchrony, < 20%; low synchrony, 20–60%; and high synchrony, > 60%.

The monthly similarity of the phenology was evaluated among the areas and the phenological diversity was evaluated within each area of the studied environments using the categories of Fournier. The individuals were characterized by the combination of categories (0, 1, 2, 3 and 4) corresponding to the phenophases encountered, which were classified into vegetative and reproductive "phenological states" (Goulart *et al.* 2005). After characterizing each sampled individual, the phenological diversity and similarity were estimated for the caatinga, savanna/caatinga transition and savanna using the Shannon-Wiener and Morisita-Horne indices, respectively. Those indices are widely used in floristic surveys and were adopted by Goulart *et al.* (2005) for phenology, where the frequency of individuals in different "phenological states" (obtained by combining

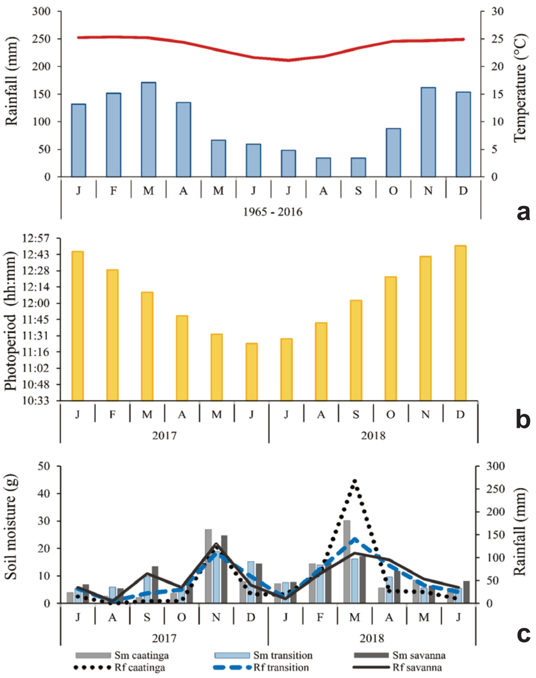

Figure 2 – Climatic data for the municipalities of Lençóis and Palmeiras, Chapada Diamantina, Bahia, Brazil. a. Historical annual averages of total rainfall and temperature from 1965 to 2016 (INMET); b. Monthly photoperiod averages (Jul/2017 to Jun/2018); c.Soil moisture (Sm) averages (columns) and monthly total rainfall (Pc) (lines) of the study areas (Jul/2017 to Jun/2018).

categories) substitutes the frequency of the different species in the community.

Data analysis

The normality of the phenological data was tested based on Shapiro & Wilk (Zar 2010). The test showed a normal distribution for the vegetative data and a non-normal distribution for the reproductive data. The influences of the abiotic factors (rainfall, average temperature, photoperiod, and soil moisture) on the vegetative phenophases were analyzed using multiple regression in the R (version 3.1.0) environment for Windows (R Core Team 2014), considering the independence assumptions of the predictor variables, normality, and homogeneity of the residues. Due to the non-normality of the data, the Spearman correlation coefficient (rs) was calculated to evaluate the influence of the abiotic factors on the reproductive phenophases, which was done using the free BioStat 5.8.3.1 software (Analystsoft 2009). The seasonality of the reproductive phenophases during the observation period in the three areas was verified with circular statistics using the Oriana program (Kovach 2004; Morellato *et al.* 2010). The following procedures were adopted: a) for the observation year, the frequency of occurrence of the phenological event of the species for each month was calculated; b) the months were converted to angles, where 15º = January and the successive months were calculated at an interval of 30º; c) the average angle, concentration, average group, angular standard deviation and length of the vector r were calculated; and d) the Rayleigh test (z and p), which is used to test the uniform distribution of circular data. Phenophases that were considered seasonal had a vector length (r) greater/equal to 0.5 ($r > 0.5$) and were significant based on the Rayleigh test ($p < 0.05$) (Zar 2010). Phenophases with a significant average angle ($p < 0.05$) were converted to an average date, or the most probable date the species would be found in each phenophase during the year.

To describe the vegetative and reproductive phenological variability of the populations, based on the categorization of the individuals into phenological states, we did and/or considered the following: (a) calculated the Shannon-Wiener diversity index using the equation proposed by Magurran (1988); (b) in practice, values assumed by the Shannon-Wiener index are between 1.5 and 3.5, and can reach 4.5, and low values indicate low diversity (Magurran 1988); (c) using the diversity index, partitioning of total diversity was determined (Htotal), from which one can ascertain the percentage of total phenological diversity that is due to differences in the behavior of individuals within a population or among populations (Lacerda *et al.* 2001); and (d) calculated the Morisita-Horn similarity index, a widely recommended quantitative index that is independent of species diversity (Wolda 1981) and varies between 0 and 1, indicating a greater (1) or lesser (0) degree of similarity in the phenological states of individuals. For more details of the methodology see Goulart *et al.* (2005).

Results

Vegetative phenology

The vegetative phenophases of *Croton heliotropiifolius* exhibited distinct intensities and synchronies in the caatinga, transition site, and savanna sites (Fig. 3). The caatinga specimens

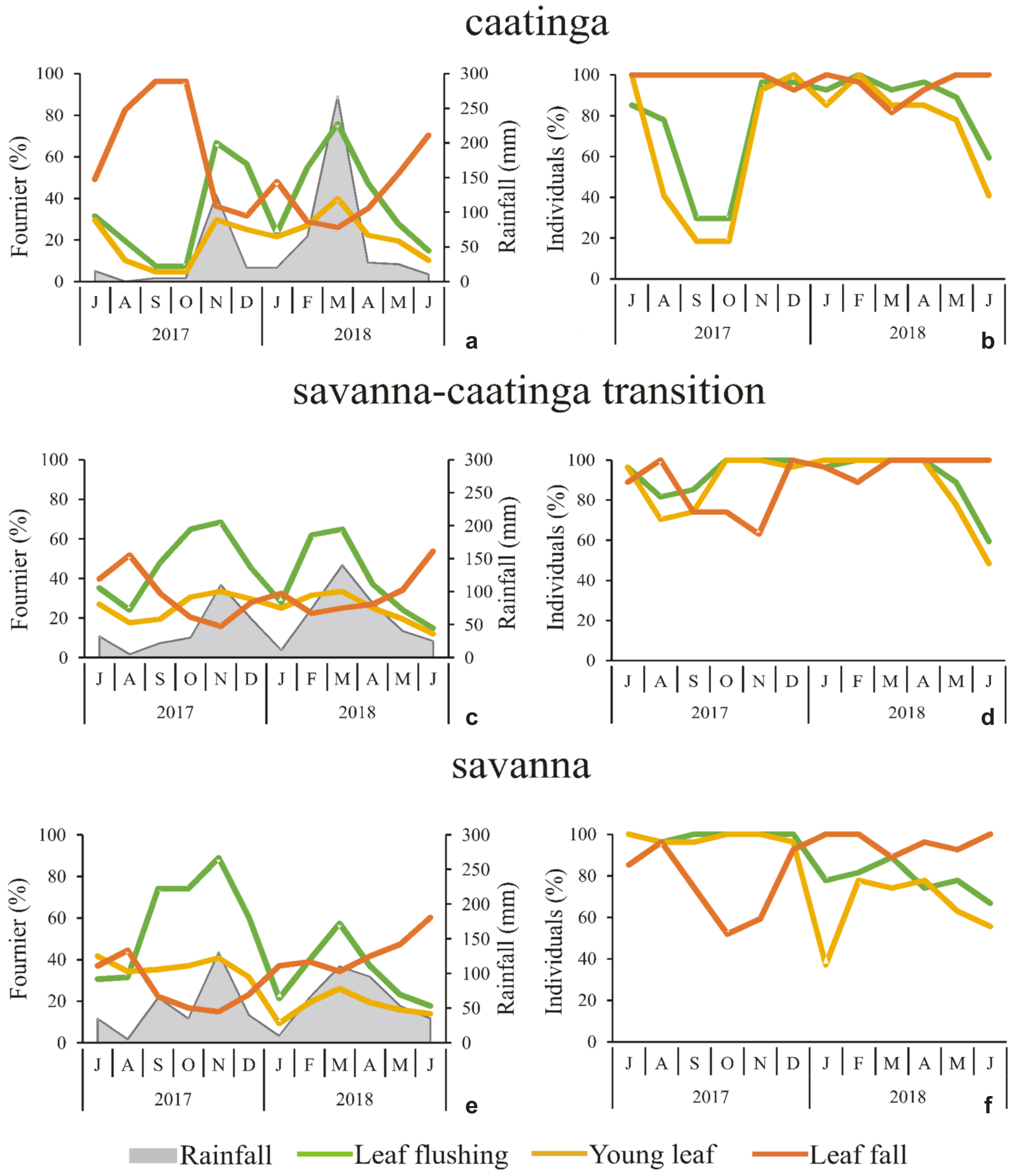

Figure 3 – Phenology and intraspecific synchrony of the vegetative phenophases (leaf flushing, young leaves, leaf fall) of *Croton heliotropiifolius* in areas of caatinga (a-b), savanna/caatinga transition (c-d) and savanna (e-f), from Jul/2017 to Jun/2018. Palmeiras, Chapada Diamantina, Bahia, Brazil.

exhibited a marked rhythm of leaf fall during the dry season (August to October), with greater leaf flushing from November to April during the rainy season (Fig. 3a). Inversely, the savanna specimens showed a marked leaf flushing rhythm that was most intense from September to December, while the production of young leaves and leaf fall were continuous (Fig. 3e). In the savanna/caatinga transition, all of the vegetative phases were continuous during the study period (Fig. 3c). Intraspecific synchrony of the vegetative phenophases varied from high to low in the caatinga and savanna sites, but maintained high synchrony at the transition site (Fig. 3b, d, f). Leaf flushing was related to rainfall and soil moisture in all areas (Tab. 1). Young leaf production was related to rainfall and soil moisture in the caatinga, and rainfall, photoperiod, and soil moisture in the savanna/caatinga transition; in the savanna site, that phenophase was not tied to environmental variables. Leaf fall was related to rainfall and soil moisture in the caatinga, and to all parameters analyzed in the transition area, including temperature, which showed no relationship to the other phenophases; in the savanna, leaf fall was related to photoperiod (Tab. 1).

Reproductive phenology

Croton heliotropiifolius exhibited low variations of flowering and fruiting intensities and synchronies in the different sites, during the rainy season (Figs. 4, 5). We observed a flowering peak in November 2017 and a secondary peak between February and May/2018 (Fig. 4). The period of greatest intensity of fruit production by *C. heliotropiifolius* was recorded between December/2017 and March/2018 (Fig. 5), with that phenophase varying from asynchronous to highly synchronous in all areas (Figs. 4, 5). The concentration coefficients were distinct in the three different sites, with marked seasonality in the savanna/caatinga transition and caatinga, but only for flowering in the savanna site (Tab. 2). All of the reproductive phenophases in the caatinga were correlated with rainfall and soil moisture (Tab. 3). In the transition site, flower budding was correlated with rainfall, soil moisture, and photoperiod; female flower production was correlated with rainfall and soil moisture, and male flower production with rainfall; immature fruit production was correlated with soil moisture. In the savanna, flower budding was correlated with rainfall and soil moisture; flowering was correlated

Table 1 – Results of the multiple regression analysis of the Fournier intensities of the vegetative phenophases of *Croton heliotropiifolius* as a function of rainfall, temperature, photoperiod and soil moisture between July/2017 and June/2018 in areas of caatinga, savanna-caatinga transition and savanna, Chapada Diamantina, Brazil. Values showing significant results (p <0.05).

Areas	**Phenophases**	**Abiotic factors**			
		Rainfall	**Temperature**	**Photoperiod**	**Soil moisture**
		p	p	p	p
caatinga	Leaf flushing	0.003	-	-	0.001
	Young leaf	0.007	-	-	0.005
	Leaf fall	0.048	-	-	0.025
savanna-caatinga transition	Leaf flushing	0.018	-	-	0.009
	Young leaf	0.013	-	0.013	0.014
	Leaf fall	0.024	0.044	0.010	0.016
savanna	Leaf flushing	0.045	-	-	0.013
	Young leaf	-	-	-	-
	Leaf fall	-	-	0.012	-

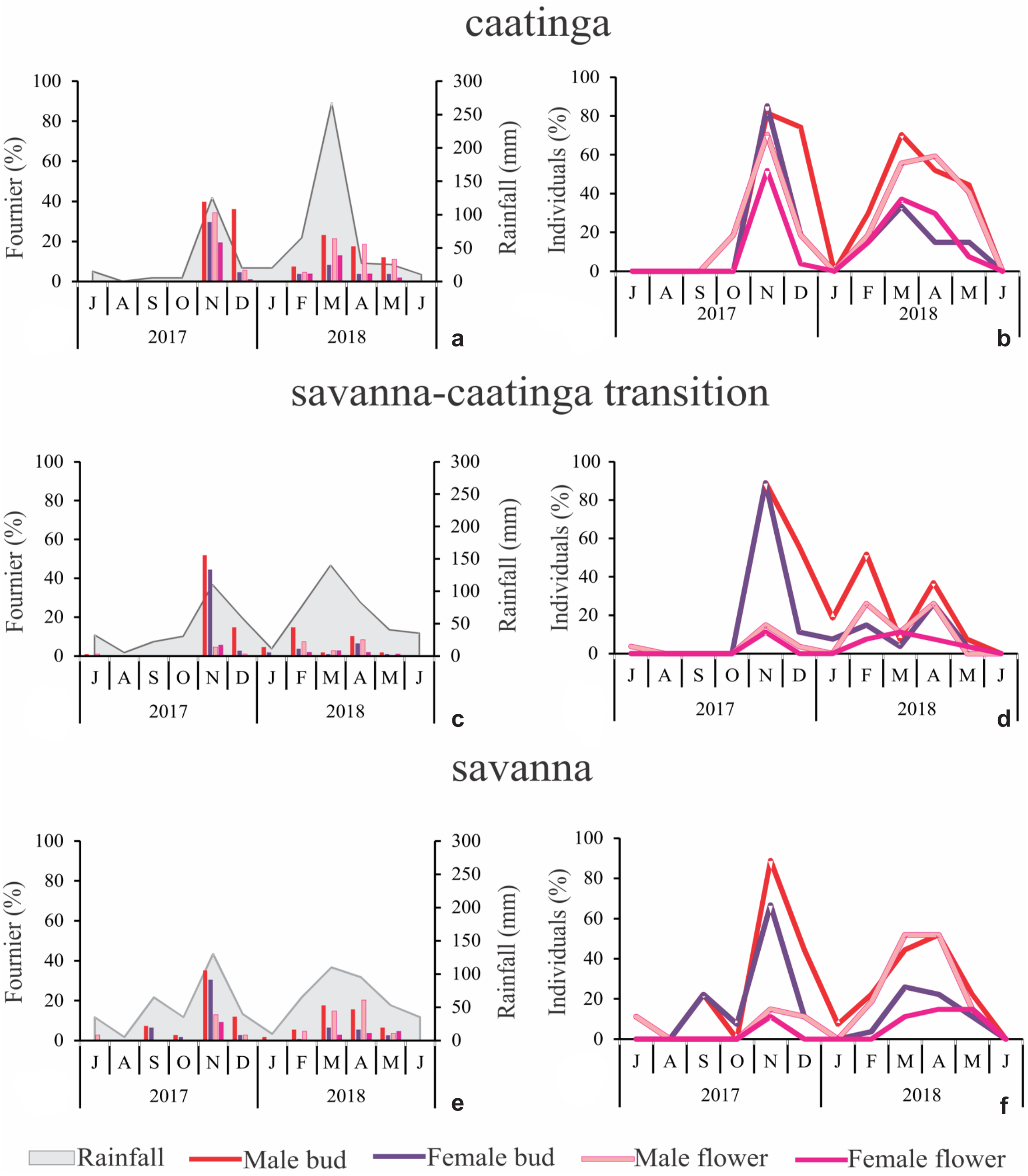

Figure 4 – Phenology and intraspecific synchrony of the reproductive phenophases (female and male buds, female and male flowers) of *Croton heliotropiifolius* in areas of caatinga (a-b), savanna/caatinga transition (c-d) and savanna (e-f), from Jul/2017 to Jun/2018. Palmeiras, Chapada Diamantina, Bahia, Brazil.

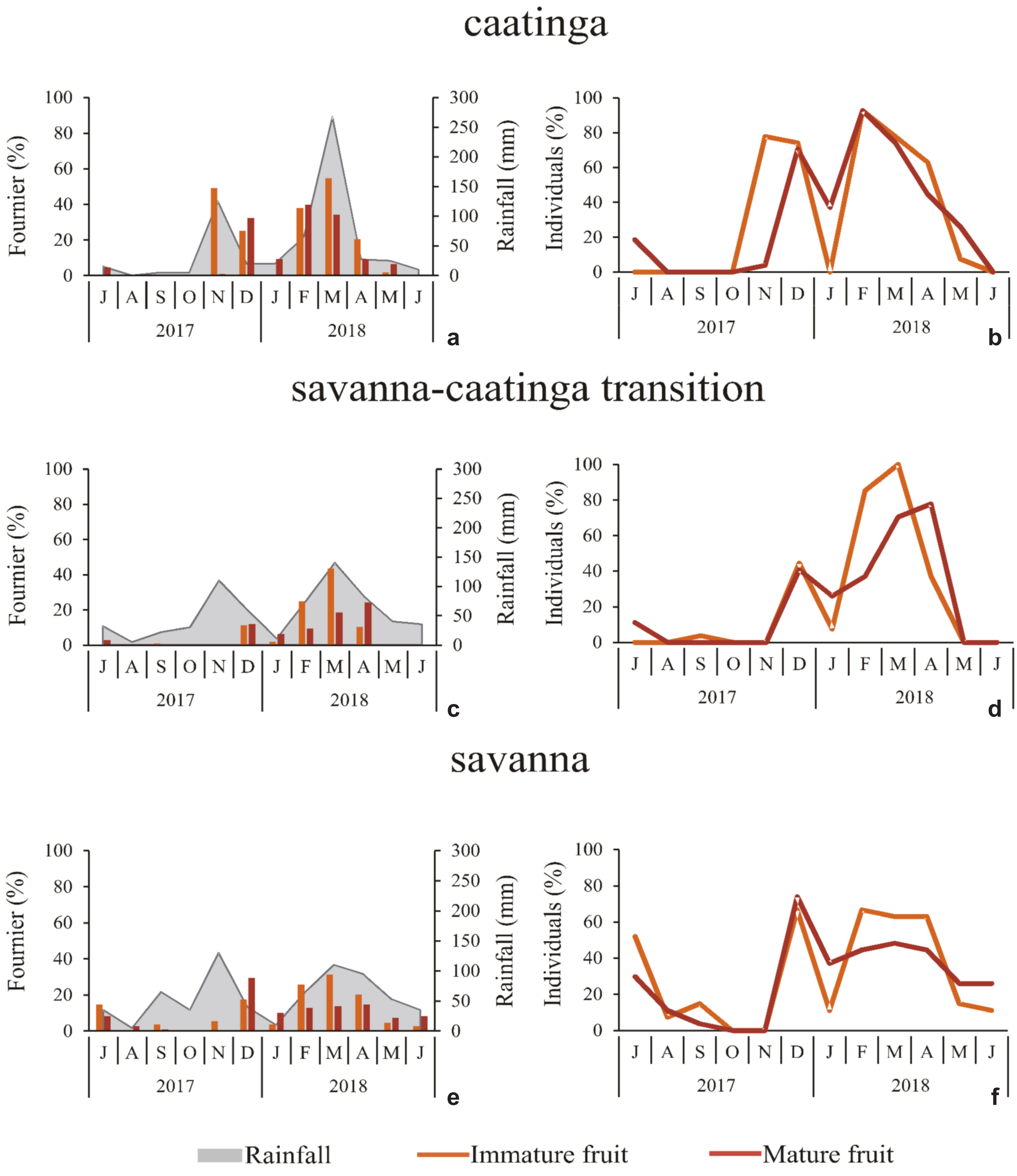

Figure 5 – Phenology and intraspecific synchrony of the reproductive phenophases (immature and mature fruits) of *Croton heliotropiifolius* in areas of caatinga (a-b), savanna/caatinga transition (c-d) and savanna (e-f), from Jul/2017 to Jun/2018. Palmeiras, Chapada Diamantina, Bahia, Brazil.

Table 2 – Circular statistics for flowering and fruiting of *Croton heliotropiifolius* from July 2017 to June 2018, sampled in savanna, savanna-caatinga transition and caatinga, Chapada Diamantina, Brazil. LMV = length of mean vector (r). Values indicating seasonality in bold (r>0.5).

Areas	Variables	Reproductive phenophases					
		Male bud	**Female bud**	**Male flower**	**Female flower**	**Immature fruit**	**Mature fruit**
caatinga	N° of observations	351	182	283	145	393	367
	LMV (r)	0.447	0.462	0.352	0.448	0.599	0.638
	Circular deviation	72.725°	71.188°	82.786°	72.646°	57.993°	54.364°
	Mean data	07 feb.	02 jan.	25 feb.	11 feb.	04 feb	22 feb.
	Mean Vector (μ)	37.197°	1.761°	55.048°	41.441°	34.724°	51.824°
	Rayleigh Test (Z)	70.085	38.873	35.084	29.053	141.078	149.169
	Rayleigh Test (p)	< 1E-12	< 1E-12	< 1E-12	< 1E-12	< 1E-12	< 1E-12
savanna-caatinga transition	N° of observations	271	156	86	40	277	263
	LMV (r)	0.582	0.552	0.570	0.519	0.796	0.693
	Circular deviation	59.612°	62.433°	60.754°	65.582°	38.652°	49.051°
	Mean data	04 jan.	10 dec.	28 feb.	26 feb.	24 feb.	04 mar.
	Mean Vector (μ)	3.926°	345.341°	58.792°	57.834°	55.15°	64.291°
	Rayleigh Test (Z)	91.803	47.583	27.938	10.791	175.725	126.372
	Rayleigh Test (p)	< 1E-12	< 1E-12	< 1E-12	1.02E-05	< 1E-12	< 1E-12
savanna	N° of observations	302	170	175	52	371	344
	LMV (r)	0.364	0.324	0.630	0.549	0.386	0.382
	Circular deviation	81.457°	85.972°	55.059°	62.774°	79.035°	79.516°
	Mean data	17 jan.	02 dec.	24 mar.	08 apr.	13 mar.	04 mar.
	Mean Vector (μ)	16.07°	337.045°	82.922°	97.873°	72.571°	63.427°
	Rayleigh Test (Z)	40.014	17.891	69.500	15.657	55.334	50.129
	Rayleigh Test (p)	< 1E-12	0.000000017	< 1E-12	1.59E-07	< 1E-12	< 1E-12

Table 3 – Results of the correlation analysis of the Fournier intensities for the reproductive phenophases of *Croton heliotropiifolius* as a function of rainfall, photoperiod and soil moisture between July/2017 and June/2018 in areas of caatinga, savanna-caatinga transition and savanna, Chapada Diamantina, Brazil, indicating the correlation coefficient (r) with which a given phenological variable follows a given meteorological variable. The correlation coefficients are significant ($p<0.05$).

		Abiotic factors					
Areas	**Phenophases**	**Rainfall**		**Photoperiod**		**Soil moisture**	
		p	**r**	**p**	**r**	**p**	**r**
caatinga	Male bud	0.0018	0.7997	-	-	0.0022	0.7913
	Female bud	0.0004	0.8552	-	-	0.0004	0.8578
	Male flower	0.0002	0.8708	-	-	0.0013	0.8136
	Female flower	<0.0001	0.9176	-	-	0.0004	0.8527
	Immature fruit	<0.0001	0.8970	-	-	0.0002	0.8808
	Mature fruit	0.0033	0.7711	-	-	0.0051	0.7488
savanna-caatinga transition	Male bud	0.0114	0.6989	0.0224	0.6490	0.0073	0.7274
	Female bud	0.0119	0.6961	0.0355	0.6091	0.0052	0.7469
	Male flower	0.0007	0.8377	-	-	-	-
	Female flower	0.0004	0.8557	-	-	0.0166	0.6721
	Immature fruit	-	-	-	-	0.0255	0.6382
	Mature fruit	-	-	-	-	-	-
savanna	Male bud	<0.0001	0.8952	-	-	0.0046	0.7535
	Female bud	0.0001	0.8831	-	-	0.0127	0.6918
	Male flower	0.0015	0.8062	-	-	-	-
	Female flower	0.0104	0.7051	-	-	-	-
	Immature fruit	0.0133	0.6885	-	-	0.0275	0.6316
	Mature fruit	-	-	-	-	-	-

with rainfall; immature fruit production was correlated with rainfall and soil moisture. Mature fruit production was not correlated with any of the parameters analyzed in the transition or savanna areas (Tab. 3). The reproductive phenophases were not related to temperature.

Phenological diversity

The *Croton heliotropiifolius* populations exhibited relatively constant levels of vegetative phenological diversity along the year, except in the caatinga during the dry season (Fig. 6a). The highest monthly diversity values were 2.65 for the savanna, 2.36 for the transition site, and 2.34 for the caatinga, during the rainy season. The lowest diversity value was seen in the caatinga (1.11), during the dry season when the leaf exchanges were strongly reduced. Reproductive phenological diversity varied along the studied period, likewise maintaining similar variation patterns in all three sites (Fig. 6b). The smallest values of reproductive phenological diversity were recorded during the dry season, varying from 0.00 in the caatinga and transition sites to 0.35 in the savanna site; the highest diversity values were seen during the rainy season (3.19 in the caatinga, 2.85 in the savanna, and 2.50 in the transition area). Phenological diversity partitioning of the vegetative phenophases

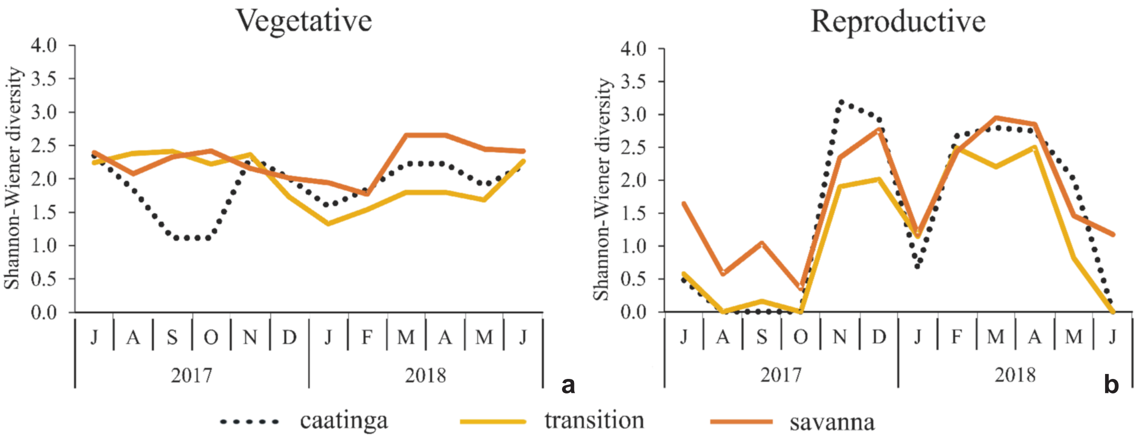

Figure 6 – Vegetative (a) and reproductive (b) phenological diversity (Shannon-Wiener index) for the populations of *Croton heliotropiifolius* in areas of caatinga, savanna/caatinga transition and savanna. Palmeiras, Chapada Diamantina, Bahia, Brazil.

was high between populations (51.20 ± 10.98%) but low within populations (48.8 ± 10.51%). Diversity partitioning of the reproductive phenophases, on the other hand, was high within populations (60.10 ± 24.60%) but low between populations (40.13 ± 23.64%).

Phenological similarity

On average, the similarity indices of the populations studied were low for vegetative (0.061 ± 0.001) and reproductive (0.249 ± 0.074) phenophases. Table 4 indicates low vegetative similarity throughout the observation period, but with no similarity during the months of September and October (during the dry season), when only the savanna and savanna/caatinga transition populations demonstrated leaf production activity. In terms of reproductive phenophases, the highest indices occurred from August to October, during the dry season, when *C. heliotropiifolius* shows almost no reproductive activity (Tab. 4).

Discussion

Our results support the initial hypothesis of this study. We found greater seasonality and synchrony in the caatinga and savanna/caatinga transition areas, with adjustment in their phenophases of leaf and floral bud production during the period when water was available to the plants. The vegetative and reproductive phenological behaviors of *C. heliotropiifolius* in the caatinga, savanna/caatinga transition, and savanna exhibited distinct intensities, seasonalities, and synchronies. The phenological events were especially related to rainfall and soil moisture, consequently, water availability in the soil in the habitats evaluated. Studies concerning variations in phenological behavior within and between populations and their habitats can help explain the extent of phenological variability as a survival strategy in different environments (Goulart *et al.* 2005; Santos *et al*. 2020), as well as how local abiotic factors influence phenological patterns (Moraes *et al.* 2017; Neves *et al.* 2017; Menezes *et al.* 2018). We analyzed variations in vegetative and reproductive phenological behaviors in habitats that were adjacent but that differed in terms of water availability – as savanna areas can be moister than caatinga sites, even when both habitats are nearly contiguous (Neves *et al.* 2017).

The leaf phenology of *C. heliotropiifolius* was marked by the climatic seasonality in the caatinga, corroborating research in dry tropical habitats that have shown that the vegetative phenology there is determined mainly by seasonal variations in water stress during the dry season, and dependent on soil water storage (Borchert *et al.* 2005; Lima & Rodal 2010; Rocha *et al.* 2015; Neves *et al.* 2016; Santos *et al*. 2020; Santos *et al*. in press). Leaf fall during the dry season reduces plant water losses and can allow it to recover water needed for leaf flushing as the dry season ends, facilitating rehydration during

Table 4 –- Morisita-Horn similarity index for vegetative and reproductive phenology of individuals of *Croton heliotropiifolius* in the caatinga, savanna-caatinga transition and savanna, Chapada Diamantina, Brazil. Averages and standard deviation (±) for 12 months (data collected from July 2017 to June 2018). Values from 0 to 1 indicate lowest to highest in the similarity index.

Years	**Month**	**Similarity (Morisita-Horn)**	
		Vegetative	**Reproductive**
2017	J	0.043	0.001
	A	0.027	0.623
	S	0.000	0.512
	O	0.000	0.634
	N	0.034	0.005
	D	0.115	0.022
2018	J	0.057	0.349
	F	0.106	0.011
	M	0.031	0.002
	A	0.120	0.016
	M	0.039	0.244
	J	0.037	0.569
Mean ± standard deviation		**0.061 ± 0.001**	**0.249 ± 0.074**

the early growing season (Reich & Borchert 1984; 1988; Franco *et al.* 2005; Rossatto *et al.* 2010; Alberton *et al.* 2014; Camargo *et al.* 2018; Santos *et al*. 2020; Santos *et al*. in press).

Although the savanna/caatinga transition area was most floristically and physiognomically similar to the caatinga (Neves *et al.* 2016), the vegetative and reproductive phenological behaviors of *C. heliotropiifolius* in the transition area were more similar in intensity, frequency, and duration to the savanna population. *C. heliotropiifolius* exhibited a continuous leaf rhythm, revealing water availability in the soil that maintains a positive hydric balance throughout the year (as seen in other cerrado plants; Prado *et al.* 2004; Rossatto 2013). Evergreen leaf habits in savanna shrub-arboreal species are a consequence of morphofunctional mechanisms that allow them to survive during the dry season (Franco *et al.* 2005; Souza *et al.* 2011; Scalon *et al.* 2017). In the savanna habitat, *C. heliotropiifolius* exhibited more intense episodes of leaf flushing in the rainy season, when there are always young leaves and low leaf fall. According to Lenza & Klink (2006), studies of savanna environments in Brazil showed that leaf loss or replacement during the dry season acts as an additional mechanism to reduce water losses.

For *C. heliotropiifolius* in the studied areas, increases in flower production are associated with water availability, independent of the intensity of rainfall – which demonstrates the importance of rainfall to the occurrence and intensity of reproductive events. This response is most expressive in the caatinga, including for Euphorbiaceae species, as Neves *et al.* (2010) found for *Jatropha* (*J. ribifolia*, *J. mutabilis* and *J. mollissima*) populations. Many dry forest species show peak flowering in the dry season (Berlin *et al*. 2000; Justiniano & Fredericksen 2000; Tesfaye *et al.* 2011), especially during the transition from the dry season to the rainy season (the time of the year when both the photoperiod and temperature increase) (Lenza & Klink 2006; Figueiredo 2008; Pirani *et al.* 2009; Borges & Prado 2014; Dalmolin *et al.* 2015; Ryan *et al.* 2017).

The populations of *C. heliotropiifolius* evaluated showed only small differences in their reproductive phenological events, which were in the starting, peak and intensity dates, and may represent levels of adaptation and adjustments to habitat conditions (Pellissier *et al.* 2014; Panchen & Gorelick 2016; Moraes *et al.* 2017). In our study, we observed more variability in vegetative phenology within and between populations, similar to the results obtained for *Plathymenia reticulata* (Fabaceae) populations in a savanna/Atlantic forest gradient - the only study that used the same phenological diversity and similarity indices employed here (Goulart *et al*. 2005).

The diversity indices of vegetative phenological behaviors were generally high in the study areas, except in the caatinga site in the dry months, which showed an expressive decrease in diversity, as *Maprounea guianensis* Aubl. (Euphorbiaceae) also showed in the caatinga vegetation (Santos *et al.* 2020). *C. heliotropiifolius* did not exhibit expressive similarity in terms of its vegetative phenophases; the lowest values were seen in the driest months. Similar results were observed for *P. reticulata*, whose vegetative phenology in the dry season was marked by high diversity within populations and low similarity between them (Goulart *et al*. 2005). The reproductive phenological diversity observed in *C. heliotropiifolius* was higher during the dry season and lower during the rainy season. Similar to our results, Goulart *et al*. (2005) found high reproductive diversity during the transition from the dry season to the rainy season, and low diversity during the dry season, with high similarity in the dry season and low similarity in the rainy season. Reproductive similarities in the study areas here were greater during the dry season when reproductive activity was low, which might favor changes in reproductive individuals and, consequently, an increase in similarity and loss of phenological diversity.

In terms of diversity partitioning, *C. heliotropiifolius* showed high vegetative phase diversity between populations but low diversity within populations, indicating intraspecific variations in the leaf phases strongly conditioned by water availability (Camargo *et al*. 2018). In contrast, reproductive phenology showed greater diversity within populations, with low diversity between populations that would favor pollination and reproductive success for the species (Elzinga *et al*. 2007; Morellato *et al*. 2016). Unlike our study, Goulart *et al*. (2005) observed considerable variation in *P. reticulata* in terms of the diversity percentages between and within populations.

Water availability in the savanna/caatinga gradient varies due to differences in the physical properties of the soils and differences in rainfall volume during the dry period (Neves *et al*. 2016; 2017) – which will influence the vegetative and reproductive phenologies of *C. heliotropiifolius* in the gradient. Our results showed that differences in soil types and rainfall volume in the dry season, even at small distances, make the savanna/caatinga gradient a suitable model for investigating phenological responses related to plant eco-hydrological strategies in seasonally tropical dry ecosystems. The contrasting availabilities of water showed that rainfall and soil moisture affect leaf production, leaf loss, and the emission of flowers and fruits, leading to variability among the phenological events of individuals both between and within populations - which is important for a better understanding of species with wide distributions such as like *C. heliotropiifolius*. We emphasize then the validity of employing diversity and similarity indices derived from floristic analyses to explore the variability of phenological responses (as per Goulart *et al*. 2005; Santos *et al*. 2020).

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References

Alberton B, Almeida J, Helm R, Torres RS, Menzel A & Morellato LPC. (2014) Using phenological cameras to track the green up in a cerrado savanna and its on-the-ground validation. Ecological Informatics 19: 62-70.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM & Sparovek G. (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728.

Analystsoft soft, 2009. BioStat version (5.8.3.0). Available at <https://biostat-2009.soft112.com.> Access on 10 July 2018.

Bencke CSC & Morellato PC. (2002) Comparação de dois métodos de avaliação da fenologia de plantas, sua interpretação e representação. Brazilian Journal of Botany 25: 269-275.

Berlin KE, Pratt TK, Simon JC & Kowalsky JR. (2000) Plant phenology in a cloud forest on the Island of

Maui, Hawaii. Biotropica 32: 90-99.

Borchert R & Rivera G. (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiology 21: 201-212.

Borchert R, Rivera G & Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica 34: 27-39.

Borchert R, Robertson K, Schwartz MD & Williams-Linera, G. (2005) Phenology of temperate trees in tropical climates. International Journal of Biometeorology 50: 57-65.

Borchert R. (1998) Responses of tropical trees to rainfall seasonality and its long-term changes 39: 381-393.

Borges MP & Prado CHB. (2014) Relationships between leaf deciduousness and flowering traits of woody species in the Brazilian neotropical savanna. Flora 209: 73-80.

Calle Z, Schlumpberger OB, Piedrahita L, Leftin A, Hammer AS, Tye A & Borchert R (2010) Seasonal variation in daily insolation induces synchromous bud break and flowering in the tropics. Trees Structure and Function 24: 865-877.

Camargo MGG, Carvalho GH, Alberton BC, Reys P & Morellato LPC (2018) Leafing patterns and leaf exchange strategies of a cerrado woody community. Biotropica 50: 442-454.

Capuzzo JP, Rossatto DR & Franco AC (2012) Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence. Acta Botanica Brasilica 26: 519-526.

Cardoso FCG, Marques R, Botosso PC & Marques MCM (2012) Stem growth and phenology of two tropical trees in contrasting soil conditions. Plant and Soil 354: 269-281.

Carneiro-Torres DS (2009) Diversidade de *Croton* L. (Euphorbiaceae) no bioma Caatinga. PhD Thesis, State University of Feira de Santana, Bahia, Brazil, 296p.

Coelho M, Fernandes WG & Sánchez-Azofeifa A (2013) Brazilian tropical dry forest on basalt and limestone outcrops: status of knowledge and perspectives. *In*: Sanchez-Azofeifa A, Powers JS, Fernandes GW & Quesada M. (eds.), Tropical dry forests in the Americas: ecology, conservation, and management. CRC Press, Boca Raton. Pp. 55-68.

Dalmolin AC, Lobo FA, Vourlitis G, Silva PR, Dalmagro HJ, Antunes Jr. MZ & Ortíz CR (2015) Is the dry season an important driver of phenology and growth for two Brazilian savanna tree species with contrasting leaf habits? Plant Ecology 216: 407-417.

Elzinga JA, Atlan A, Biere A, Gigord L, Weis AE & Bernasconi G (2007) Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22: 432-439.

Embrapa (2011) Manual de métodos de análise de solo. 2 ed. Revista Embrapa Solos. Rio de Janeiro. 212p.

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.

Flora do Brasil 2020. Croton. *In*: Flora of Brasil 2020. Botanic Garden of Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB17497>. Access on 10 June 2020.

Fournier, LA (1974) Un método cuantitativo para la medición de características fenológicas en árboles. Turrialba 24: 422-423.

Franco AC, Bustamante MM, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P & Coradin VTR (2005) Leaf functional traits of neotropical savanna trees in relation to seasonal water deficit. Trees Structure and Function 19: 326-335.

Funch LS, Funch RR & Barroso GM (2002) Phenology of gallery and montane forest in the Chapada Diamantina, Bahia, Brazil. Biotropica 34: 40-50.

Funch RR, Harley RM & Funch LS (2009) Mapping and evaluation of the state of conservation of the vegetation in and surrounding the Chapada Diamantina National Park, NE, Brazil. Biota Neotropica 9: 21-30.

Goulart MF, Lemos Filho JP & Lovato MB (2005) Phenological variation within and among populations of *Plathymenia reticulata* in Brazilian savanna, the Atlantic Forest and transitional sites. Annals of Botany 96: 445-455.

Juncá FA, Funch LS & Rocha W (2005) Biodiversidade e Conservação da Chapada Diamantina. Ministério do Meio Ambiente - MMA, Brasília. 436p.

Justiniano M & Fredericksen T (2000) Phenology of tree species in Bolivian dry forests. Biotropica 32: 276-280.

Kovach WL (2004) Oriana–Circular Statistics for Windows. Ver. 4. Kovach Computing Services: Pentraeth.

Lacerda DMA, Barros JBHA, Almeida EB & Rossatto DR (2017) Do conspecific populations exhibit divergent phenological patterns? A study case of widespread Savanna species. Flora 236-237: 100-106.

Lacerda DMA, Rossatto DR, Ribeiro-Novaes EKMD & Almeida Jr. EB (2018) Reproductive phenology differs between evergreen and deciduous species in a Northeast Brazilian Savanna. Acta Botanica Brasilica 32(3): 367-375.

Lacerda DR, Acedo MDP, Lemos Filho JP & Lovato MB (2001) Genetic diversity and structure of natural populations of *Plathymenia reticulata* (Mimosoideae), a tropical tree from the Brazilian Savanna. Molecular Ecology 10: 1143-1152.

Lemos Filho JP, Goulart MF & Lovato MB (2008)

Populational approach in ecophysiological studies: the case of *Plathymenia reticulata*, a tree from Savanna and Atlantic Forest. Brazilian Journal of Plant Physiology 20: 205-216.

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.

Lieth H (1974) Purpose of a phenology book. In: Lieth H. (ed.). Phenology and seasonality modeling. Springer-Verlag, Berlin. Pp. 3-19.

Lima ALA & Rodal MJN (2010) Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil. Journal of Arid Environments 74: 1363-1373.

Lima ALA, Sampaio EVSB, 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 Structure and Function 26: 1605-1616.

Lima LRD & Pirani JR. (2008). Taxonomic revision of Croton sect. Lamprocroton (Müll. Arg.) Pax (Euphorbiaceae s.s.). Biota Neotropica 8: 177-215.

Magurran AE (1988) Ecological diversity and its measurement. Cambridge University Press, Cambridge. 192p.

Menezes IS, Couto-Santos APL & Funch LS (2018) The influence of *El Niño* and edge effects on the reproductive phenology and floral visitors *of Eschweilera tetrapetala* Mori (Lecythidaceae), an endemic species of the Atlantic forest of northeastern Brazil. Acta Botanica Brasilica 32: 1-11.

Miranda LAP, Vitória AP & Funch LS (2011) Leaf phenology and water potential of five arboreal species in gallery and montane forests in the Chapada Diamantina, Bahia, Brazil. Environmental and Experimental Botany 70: 143-150.

Mitchell RM & Bakker JD (2014) Intraspecific trait variation driven by plasticity and ontogeny in Hypochaeris radicata. Plos One 9(10): e109870.

Moraes ACS, Vitória AP, Rossatto DR & Funch LS (2017) Leaf phenology and morphofunctional variation in *Myrcia amazonica* DC. (Myrtaceae) in gallery forest and ‘‘campo rupestre’’ vegetation in the Chapada Diamantina, Brazil. Brazilian Journal of Botany 40: 439-450.

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. Springer, New York. Pp. 357-371.

Morellato LPC, Alberton B, Alvarado ST, Borges B, Buisson E, Camargo MGG, Cancian LF, Carstensen DW, Escobar DFE, Leite PTP, Mendoza I, Rocha NMWB, Soares NC, Silva TSF, Staggemeier VG, Streher AS, Vargas BC & Peres CA (2016) Linking plant phenology to conservation biology. Biological Conservation 195: 60-72.

Morellato LPC, Camargo MGG & Gressler E (2013) A review of plant phenology in South and Central America. In: Schwartz MD. (ed.) Phenology: An Integrative Environmental Science. Springer, The Neederlands. Pp. 91-113.

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.

Neves SPS, Funch RR, Conceição AA, Miranda LAP & Funch LS (2016) What are the most important factors determining different vegetation types in the Chapada Diamantina, Brazil. Brazilian Journal Biology 76: 315-333.

Neves SPS, Miranda LAP, Rossatto DR & Funch LS (2017) The roles of rainfall, soil properties, and species traits in flowering phenology along a savanna-seasonally dry tropical forest gradiente. Brazilian Journal of Botany 40: 665-679.

Oliveira DD, Silva CV, Guedes MLS & Velozo ES. (2016). Fixed and volatile constituents of *Croton heliotropiifolius* Kunth from Bahia-Brazil. African Journal of Pharmacy and Pharmacology 10: 540-545.

Panchen ZA & Gorelick R (2016) Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the Mid-Arctic. International Journal of Plant Sciences 77: 661-670.

Pellissier L, Roger A, Bilat J & Rasmann S (2014) High elevation *Plantago lanceolata* plants are less resistant to herbivory than their low elevation conspecifics: Is it just temperature? Ecography 37: 950-959.

Pennington RT, Lavin M & Oliveira Filho AT (2009) Woody plant diversity, evolution and ecology in the tropics: perspectives from seasonally dry tropical forests. Annual Review of Ecology, Evolution, and Systematics 40: 437-457.

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.

Prado CHBA, Wenhui Z, Cardoza Rojas MH & Souza GM (2004) Seasonal leaf gas exchange and water potential in a woody Cerrado species community. Brazilian Journal of Plant Physiology 16: 7-16.

R Core Team. 2014. R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Radulovic N, Mananjarasoa E, Harinantenaina L & Yoshinori A. (2006). Essential oil composition of four Croton species from Madagascar and their chemotaxonomy. Biochemical Systematics and Ecology 34: 648-653.

Reich PB & Borchert R (1988) Changes with leaf age in stomatal function and water status of several tropical tree species. Biotropica 20: 60-69.

Reich PB & Borchert R. (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. Journal of Ecology 72: 61-74.

Rocha TGF, Silva RAR, Dantas EX & Vieira FA (2015) Fenologia da *Copernicia prunifera* (Arecaceae) em uma área de caatinga do Rio Grande do Norte. Cerne 21: 673-682.

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.

Rossatto DR, Hoffmann WA, Silva LCR, Haridasan M & Sternberg LSL Franco AC (2013) Seasonal variation in leaf traits between congeneric savanna and forest trees in Central Brazil: implications for forest expansion into savanna. Trees 27: 1139-1150.

Rossatto DR, Takahashi FSC, Silva LCR & Franco, AC (2010) Características funcionais de folhas de sol e sombra de espécies arbóreas em uma mata de galeria no Distrito Federal, Brasil. Acta Botanica Brasilica 24: 640-647.

Ryan CM, Williams M, Grace J, Woollen E & Lehmann CER (2017) Pre-rain green up is ubiquitos acrros tropical Africa: implications for temporal niche separation and model representation. New Phytologist 213: 625-633.

San Martin-Gajardo I & Morellato LPC (2003) Fenologia de Rubiaceae do dub-bosque em floresta atlântica no sudeste do Brasil. Brazilian Journal of Botany 26: 299-309.

Sa'nchez-Azofeifa A, Calvo-Alvarado J & Espírito-Santo MM (2013) Tropical dry forest in the Americas: the trop-dry endeavor. *In*: Sanchez-Azofeifa A, Powers JS, Fernandes GW & Quesada M (eds) Tropical dry forests in the Americas: ecology, conservation, and management. CRC Press, Mexico. 556p.

Santos MGM, Neves SPS, do Couto-Santos APL, Cerqueira CO, Rossatto DR, Miranda LAP, Funch LS (2020) Phenological diversity of *Maprounea guianensis* (Euphorbiaceae) in humid and dry neotropical forests. Australian Journal of Botany 68: 288-299.

Santos MGM, Sousa AS, Neves SPS, Rossatto DR, Miranda LAP, Funch LS (in press) Drought responses and phenotypic plasticity of *Maprounea guianensis* populations in humid and dry tropical forests. Rodriguésia.

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.

Seghieri J & Simier S (2002) Variations in phenology of a residual invasive shrub species in Sahelian fallow Savannas, south-west Niger. Journal of Tropical Ecology 18: 897-912.

Silva JS, Sales MF & Carneiro-Torres DS (2009) O gênero *Croton* (Euphorbiaceae) na microrregião do Vale do Ipanema, Pernambuco, Brasil. Rodriguésia 60: 879-901.

Silva JS, Sales MF, Gomes APS & Carneiro-Torres DS (2010) Sinopse das espécies de *Croton* L. (Euphorbiaceae) no estado de Pernambuco, Brasil. Acta Botanica Brasilica 24: 441-453.

Souza IM & Funch LS (2017) Synchronization of leafing and reproductive phenological events in *Hymenaea* L. species (Leguminosae, Caesalpinioideae): the role of photoperiod as the trigger. Brazilian Journal of Botany 40: 125-136.

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.

Tesfaye G, Teketay D, Fetene M & Beck E (2011) Phenology of seven indigenous tree species in a dry afromontane forest, Southern Ethiopia. Tropical Ecology 52: 229-241.

Toledo MM, Paiva EAS, Lovato MB & Lemos Filho JP (2012) Stem radial increment of forest and Savanna ecotypes of a Neotropical tree: relationships with climate, phenology, and water potential. Trees Structure and Function 26: 1137-1144.

Vico G, Thompson SE, Manzoni S, Molini A, Albertson JD, Almeida-Cortez JS, Fay PA, Feng X, Guswa AJ, Liu H, Wilson TG & Porporato A. (2015) Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. Ecohydrology 8: 660-681.

Vilela AA, Del-Claro VTS, 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.

Wolda H (1981) Similarity Indices, Sample Size and Diversity. Oecologia (Berl) 50: 296-302.

Zar JH (2010) Biostatistical analysis. New Jersey, Prentice-Hall.

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