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VEGETATIVE PHENOLOGY IN CERRADO FOREST VEGETATION TYPES: A COMPARATIVE APPROACH

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The Cerrado vegetation types has the same macroclimate, but differs in the microclimatic and edaphic proprieties, which can result in contrasting phenologies among it. The vegetative phenology of five vegetation types such as woody savanna, deciduous and semideciduous forests, gallery forest, and riparian forest in Brazil Central plateau were accessed in this study. Leaf falls and leaf budding of 10 individuals of the 12 most abundant species were evaluated monthly in each vegetation type over one year. Circular statistics and the Rayleigh test were used to assess the phenology peaks. The average intensity rate of leaf fall and leaf budding were calculated for each vegetation type and chi-square test was used to analyse differences among them. Of the 53 species studies, 15 were deciduous, 17 semi-deciduous and 21 evergreens. All vegetation types demonstrated seasonality, reflecting the season macroclimate predominance. However, the peaks of phenophases were different between them throughout the year, which in turn reflects the effect of the microclimatic and edaphic proprieties. Our results indicated that within the same remnant a greater number of forests patches may increase phenological strategies. Thus, several vegetation types ensured resources for associated fauna and ecosystem services at different periods of the year.

Keywords: Cerrado plateau, Cerrado forests patches, forest phenology, leaf budding, leaf falls, non-reproductive phenology, resource availability

INTRODUCTION

Phenological studies are important to measure plant responses to environmental factors, because it is an indicator of plant-atmosphere (Piao et al. 2019) and plant-soil interactions (Nord & Lynch 2009). Under similar macro environmental conditions, phenological strategies may vary between forest vegetation communities as a function of several factors which matter in fine scale (Klosterman et al. 2018). These variations can be observed in the episodes of leaf budding and leaf fall, generally associated with environmental variables, such as climate and soil (Williams et al. 1999). Studies have attempted to establish relationships between phenology and local environmental conditions, such as soil and air humidity, temperature and precipitation (Borchert et al. 2004) and primary consumers (Williams et al. 1999). Soil water availability is also one of the main factors to explain phenological patterns, although it is still not very clear for tropical forests and savannas (Borchert et al. 2004).

Anthropic actions such as fragmentation, climate change, and increased on fire frequency have been modifying the phenology of plant species (Gordo & Sanz 2010, Korner & Basler 2010, Morellato et al. 2016). For example, a mechanistic model revealed change in the performance of evergreen and deciduous species in response to decreased of precipitation, increased in fire and loss of animal dispersal in Cerrado (Maciel et al. 2021). This study also showed that species performance was different across vegetation types. Although the tree phenology of different Cerrado vegetation types is well known (Oliveira 2008) a substantial part of the previous published studies are limited to species and populations (Guilherme et al. 2015, Leão-Araújo et al. 2019). Studies comparing plant communities across vegetation types under the same macroclimatic conditions are still scarce (Morellato et al. 2016), and that are almost absent in Cerrado forests patches (Camargo et al. 2018).

Forests in the Cerrado have wide environmental heterogeneity, being important for the maintenance of local diversity and ecosystem services (Nascimento et al. 2022, Souza et al. 2018). They are classified in woody savanna, dry, riparian and gallery forests (Ribeiro & Walter 2008). Woody savannas occur on flat terrain and well drained soils, with less vertical stratification, a more open canopy and irregular leaf fall relative to the others. Dry forests, semideciduous and deciduous seasonal forests occur in the interfluves well drained and rich in nutrients soils gradient, as consequence, it could be evergreen, semideciduous or deciduous according to the leaf fall level during the dry season. Riparian forests surround medium and large rivers, and become pronounced deciduous in the dry season. Gallery forests occurs as corridors along small rivers or wetlands, which ensures soil moisture even in the dry season. These are classified as non-flooded when the soil is well drained, with normally uneven topography, bordering well-defined watercourses with constant flow, while flooded presents a water in the soil almost permanently, with little defined drainage, and established on flat relief and hydromorphic soils.

Although phenological knowledge plays a key role in conservation and management strategies, it is still unclear how phenological strategies differ between Cerrado forests patches (Morellato et al. 2016, Camargo et al. 2018). Therefore, we assessed the vegetative phenology of five forest vegetation types, namely woody savanna, semideciduous and deciduous seasonal forests, riparian forest and flooded gallery forest in Brazil Central plateau over one year. This vegetation types are under the same macroclimate conditions of predominant seasonality, with well-defined dry and rainy periods (Carneiro et al. 2020). Thus, we expect that the different vegetation types behave according to macroclimate, as there is an adjustment of the vegetative events to this Cerrado seasonality (Oliveira 2008, Silvério & Lenza 2010). We also expect that each type of vegetation has a particular intensity of phenological events due to microclimatic, edaphic properties and soil moisture peculiarities (Moreno & Cardoso 2008, Ribeiro & Walter 2008). Thus, we tested the hypothesis that each vegetation type shows a seasonal rhythm that reflects an adjustment with the regional climate, but that there are differences in the vegetative phenological rhythm (leaf budding and leaf fall), as a function of adjustment to local abiotic conditions.

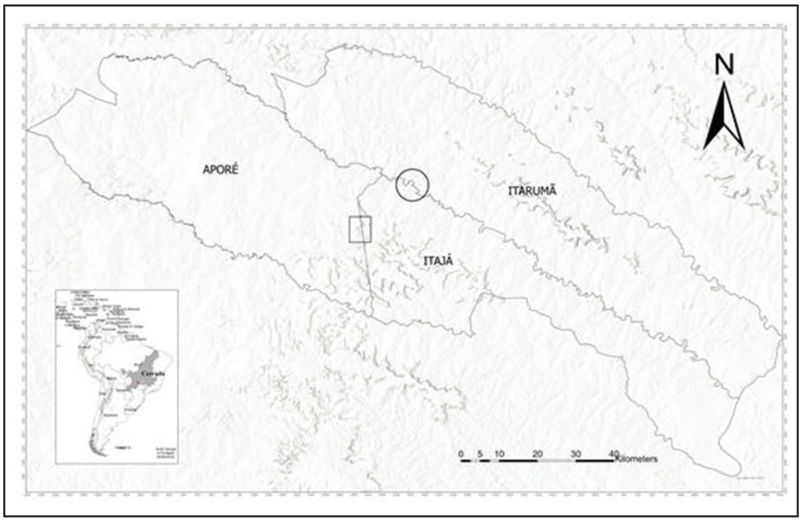

Figure 1 Map of forest remnants among the municipalities of Itajá, Aporé and Itarumã, in the southwest Goiás state, in the Cerrado-Atlantic Forest transition

The square and circle areas correspond to large (~3960 ha) and small (~1040 ha) remnants localisation, respectively; the red dot on the South America map shows the location of the municipalities where the remnants are located, emphasizing their marginal location in the Cerrado, delimited in gray

MATERIAL AND METHODS

Study site

We conducted the study in two forest remnants, surrounded by pasture matrix, in Brazil Central plateau, southwest of the Goiás state (Figure 1). Altogether, its remnants comprise native forest ecosystems of about 5000 non-continuous hectares, at coordinates 18° 55' S and 51° 42' W. These remnants are approximately 13 km apart and belong to private properties that have been the focus of other studies of our researches team of Long Term Ecological Research located in the Cerrado-Atlantic forest transition zone (PELD-CEMA), which have been provide subsidies for the implementation of the proposed Tovacuçu Wildlife Reserve (Carneiro et al. 2020). Elevations range from 480 to 650 m and the relief is characterised by steep slopes between interfluves and valley bottom. The regional climate is seasonal, tropical savanna and mesothermal, classified as Aw according to the Köppen climatic classification, wherein there are two well-defined periods, one dry (from April to September) and the other rainy (from October to March). The annual precipitation varies from 1400 to 1500 mm (Wachholz et al. 2020). December and January have the highest precipitation levels, while June to September are the driest months with the lowest relative humidity.

For the phenological study we selected five forest vegetation types typically found in the Cerrado: woody savanna (WS), semideciduous forest (SF), deciduous forest (DF), riparian forest (RF) and flooded gallery forest (GF). Only RF is located located in remnant alongside Corrente River, while the other forest patches are in the larger remnant (Figure 1). These vegetation types were classified according to the physiographic features, associated with the floristic composition of each environment (Ribeiro & Walter 2008). SF and DF are predominant in the remnant in well-drained areas and WS occurs at the edge of the remnant. Oxisols are the main soil classes in those well-drained areas, although Ultisols prevail in slightly hilly relief. GF occur in the valley bottom, with moist environments and poorly drained soils such as the Gleisoil. All the vegetation types show little or no signal of anthropic disturbance, except the WS, which is in succession due to the coffee plantations approximately 40 years ago (Guilherme et al. 2020).

Sampling

For each vegetation type we conducted the study in one-hectare permanent plots, subdivided in 25–20 × 20 m quadrats, where tree vegetation surveys were carried out (Ferreira et al. 2020, Guilherme et al. 2020, Nascimento et al. 2022, Guilherme et al. 2023). All individuals with diameter breast height ≥ 5 cm were taxonomically identified and marked with aluminium tags. These tags allowed the monthly evaluation of the same plants throughout one year. For each sample plot, we created a matrix with all species and calculated the relative density of each species. We selected the 12 most abundant (highest relative densities) in each sample plot (which together represent 50% or more of the total abundance of each vegetation types). Ten adult individuals (matrices) of each of these 12 species were selected to observe phenological patterns, thus totalling 600 trees observed during a year.

These individuals had their vegetative phenophases of leaf budding (emergence of vegetative buds followed by small leaves, usually shiny, light green, yellowish or red) and leaf fall (leaves with a change in colour, which begin to fall from the plant, forming gaps in the crown and accumulating on the ground) recorded monthly throughout the year 2019. In order to quantify the phenological events of each individual, we sampled several points around its canopy, then we used a binoculars and digital camera for observe the detailing of phenophases, especially for individuals with greater height.

We adopted the direct phenological measurement or intensity index (D'Eça-Neves & Morellato 2004), which divides the intensity of phenophases into three categories: zero (0) for absence, one (1) for up to 50% and two (2) for more than 50% intensity of each phenophase. Such a measure was used since the high canopy in forests hinders phenological estimation, allowing, at the same time, a quantitative assessment. Furthermore, this measure is efficient in capturing peaks of intensity of leaf fall and leaf budding in each population, thus helping us to observe how the intensity peaks of these phenophases vary among vegetation types (Bencke & Morellato 2002). The data from each plant in the population were then considered separately to determine the species of each vegetation types in one of the following phenophases - 1. evergreen: those that lose and sprout leaves at a uniform rate throughout the year; 2. semi-deciduous: those that lose approximately half of their leaves during the dry season; and 3. deciduous: completely deciduous plants, which occur during the dry season.

Data analysis

We used the average intensity of the ten individuals of each species in each month to describe and compare the phenodynamics between vegetation types. We multiplied the mean intensity by 100 and divided by 2 (number of intensity measurement categories), in order to convert the values into percentages (D'Eça-Neves & Morellato 2004). With this procedure we obtained the percentage intensity of each phenophase, for each species, in each month. Finally, we calculated the average of the percentage intensity of the 12 species per month.

We used circular statistics to measure the intensity and occurrence of seasonality of the two phenophases throughout the year. To do this, we followed the following procedures: (1) for each month of observation, we calculated the frequency of occurrence of the phenological for all species; (2) the months were converted into angles, being 0º = January, successively until 330º = December, in intervals of 30º; (3) we calculated the average angle and the length of the vector r and tested the significance of the angle through the Rayleigh test (z) for the circular distribution (Zar 2010). Vector r indicates how much the dates are grouped around the average angle and reflects the level of phenological seasonality or synchrony of the phenophases of each population or community (Morellato et al. 2000). We used the chi-square ($\chi 2$) test to compare the frequency of occurrences of each phenophases of each vegetation types in order to test whether the phenologies were different between them. The Oriana program was used to calculate the circular statistics (Kovach 2011).

RESULTS

General phenological patterns in Cerrado vegetation types

The 600 individuals comprised 53 species, of which seven occurred in two and the others only in one of the five vegetation types (Table 1). Fifteen of them were deciduous, 17 semi-deciduous and 21 evergreen. The relative density among species ranged from 20.46 (*Tachigali vulgaris*) to 1.77 (*Salvertia convallariodora*) in woody savanna, from 7.02 (*Cordiera sessilis*) to 2.17 (*Copaifera langsdorffii*) in semideciduous forest, from 12.3 (*Chrysophyllum marginatum*) to 5.09 (*Aspidosperma subincanum*) in deciduous forest, from 7.14 (*Cheiloclinium cognatum*) to 3.76 (*Aspidosperma polyneuron*) in riparian forest, from 43.54 (*Euterpe edulis*) to 0.55 (*Ficus enormis*) in flooded gallery forest.

The leaf budding showed a seasonality throughout the year ($z = 175.4$; $P < 0.001$; $r = 0.22$), with intensity peaks in September (40.84%), October (44.67%) and November (47.57%), i.e., the transition period between the dry and rainy seasons (Figure 2). This period was preceded by the highest leaf fall intensities which occurred between the months of July (42.33%), passing through August (49.41%) to September (45.39%), that is, in the driest period of the year (Figure 2). Therefore, leaf fall was also presented certain seasonality ($z = 163.5$; $P < 0.001$; $r = 0.21$).

Vegetative phenology among forest vegetation types

Leaf budding and leaf fall differed between the five vegetation types over the months, by $\chi 2$ test (Table 2). Regarding leaf fall pattern, woody savanna and semideciduous forest showed higher number of semideciduous species (n = 7) being *Tachigali vulgaris* and *Allophylus edulis*, respectively, the most abundant deciduous species in these forests. Riparian forest and flooded gallery forest have more species with evergreen behaviour (n = 8), such as *Cheiloclinium cognatum* and *Euterpe edulis.* Finally, deciduous forest showed more deciduous species (n = 8), being *Bauhinia membranacea* the most abundant deciduous species in this vegetation type (Table 1, Figure 3). However, when the total mean

Table 1 Species assessed by forest vegetation types of Cerrado in southwest of the Goiás state

Forest types/Species	Family	RD	Deciduousness
Woody savanna			
Tachigali vulgaris L.G.Silva & H.C.Lima	Fabaceae	20.46	Semideciduous
Emmotum nitens (Benth.) Miers	Metteniusaceae	8.91	Evergreen
Xylopia aromatica (Lam.) Mart.	Annonaceae	3.87	Semideciduous
Qualea parviflora Mart.	Vochysiaceae	5.78	Semideciduous
Qualea grandiflora Mart.	Vochysiaceae	6.25	Semideciduous
Tapirira guianensis Aubl.	Anacardiaceae	5.57	Evergreen
Roupala montana Aubl.	Proteaceae	3.81	Semideciduous
Leptolobium elegans Vogel	Fabaceae	3.26	Semideciduous
Anadenanthera falcata Speg.	Fabaceae	2.24	Deciduous
Virola sebifera Aubl.	Myristicaceae	2.11	Semideciduous
Myrcia splendens (Sw.) DC.	Myrtaceae	1.84	Deciduous
Salvertia convallariodora A.St.-Hil.	Vochysiaceae	1.77	Deciduous
Semideciduous forest			
Cordiera sessilis (Vell.) Kuntze	Rubiaceae	7.02	Evergreen
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl	Sapindaceae	6.60	Semideciduous
Trichilia casaretti C.DC.	Meliaceae	6.09	Evergreen
Cedrela fissilis Vell.	Meliaceae	3.61	Deciduous
Machaerium acutifolium Vogel	Fabaceae	3.10	Semideciduous
Coussarea hydrangeaefolia (Benth.) Müll.Arg.	Rubiaceae	2.58	Evergreen
Ouratea castaneifolia (DC.) Engl.	Ochnaceae	3.30	Evergreen
Matayba guianensis Aubl.	Sapindaceae	4.85	Semideciduous
Unonopsis guatterioides (A.DC.) R.E.Fr.	Annonaceae	2.79	Semideciduous
Aspidosperma cuspa (Kunth) Blake	Apocynaceae	2.89	Semideciduous
Copaifera langsdorffii Desf.	Fabaceae	2.17	Semideciduous
Erythroxylum sp.	Erythroxylaceae	3.30	Semideciduous
Deciduous forest			
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Sapotaceae	12.30	Semideciduous
Bauhinia membranacea Benth	Fabaceae	7.22	Deciduous
Astronium urundeuva Fr. All.	Anacardiaceae	6.53	Deciduous
Syagrus oleracea (Mart.) Becc.	Arecacae	5.36	Evergreen
Trichilia catigua A.Juss.	Meliaceae	4.74	Evergreen

continued

Table 1 Continued

Forest types/Species	Family	RD	Deciduousness
Anadenanthera colubrina (Vell.) Brenan	Fabaceae	3.23	Deciduous
Tabebuia roseoalba (Ridl.) Sandwith	Bignoniaceae	3.09	Deciduous
Terminalia argentea Mart.	Combretaceae	5.15	Deciduous
Sweetia fruticosa Spreng.	Fabaceae	3.16	Deciduous
Cordiera sessilis (Vell.) Kuntze	Rubiaceae	1.58	Semideciduous
Jacaranda cuspidifolia Mart.	Bignoniaceae	1.65	Deciduous
Aspidosperma subincanum Mart.	Apocynaceae	5.09	Deciduous
Riparian forest			
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae	7.14	Evergreen
Unonopsis guatterioides (A.DC.) R.E.Fr.	Annonaceae	5.36	Semideciduous
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl	Sapindaceae	4.61	Semideciduous
Trichilia casaretti C.DC.	Meliaceae	3.95	Evergreen
Garcinia brasiliensis Mart.	Clusiaceae	6.02	Evergreen
Ixora brevifolia Benth.	Rubiaceae	4.70	Evergreen
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	3.29	Evergreen
Hirtella gracilipes (Hook.f.) Prance	Chrysobalanaceae	2.91	Semideciduous
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	4.04	Deciduous
Trichilia claussenii C.DC.	Meliaceae	2.91	Evergreen
Guarea guidonia (L.) Sleumer	Meliaceae	2.82	Evergreen
Aspidosperma polyneuron Mülle.Arg.	Apocynaceae	3.76	Evergreen
Gallery forest			
Euterpe edulis Mart.	Arecaceae	43.54	Evergreen
Tapirira guianensis Aubl.	Anacardiaceae	11.35	Semideciduous
Calophyllum brasiliense Cambess	Calophyllaceae	5.09	Evergreen
Cedrela odorata L.	Meliaceae	4.88	Deciduous
Dendropanax cuneatus (DC.) Decne. & Planch	Araliaceae	3.65	Evergreen
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	3.37	Evergreen
Casearia gossypiosperma Briq.	Salicaceae	3.16	Semideciduous
Guarea guidonia (L.) Sleumer	Meliaceae	0.83	Evergreen
Tabebuia insignis (Miq.) Sandwith	Bignoniaceae	2.41	Deciduous
Magnolia ovata A.St.-Hil. (Spreng.)	Magnoliaceae	3.03	Evergreen
Xylopia emarginata Mart.	Annonaceae	0.96	Evergreen
Ficus enormis Mart. ex Miq.	Moraceae	0.55	Evergreen

RD = relative density referring to the total abundance in a hectare, and functional attribute related to leaf fall (deciduousness)

Table 2 Matrix of comparisons of leaf budding (in bold) and leaf fall (without bold) between the five forest vegetation types studied in the southwest of the Goiás state

Forest types	WS	SF	DF	RF	GF
WS		**50.5*****	**57.9*****	**64.4*****	**68.8*****
SF	48.7***		**41.6*****	**91.7*****	**90.0*****
DF	87.7***	66.5***		**65.3*****	**45.5*****
RF	20.8 *	71.2***	97.0***		**47.1*****
GF	76.0***	96.3***	132.5***	67.3***	

Asterisks represent the level of significance of comparison by the $\chi 2$ test ($P < 0.05$ *; $P < 0.0001$ ***); WS = woody savanna, SF = semideciduous forest, DF = deciduous forest, RF = riparian forest, GF = gallery forest

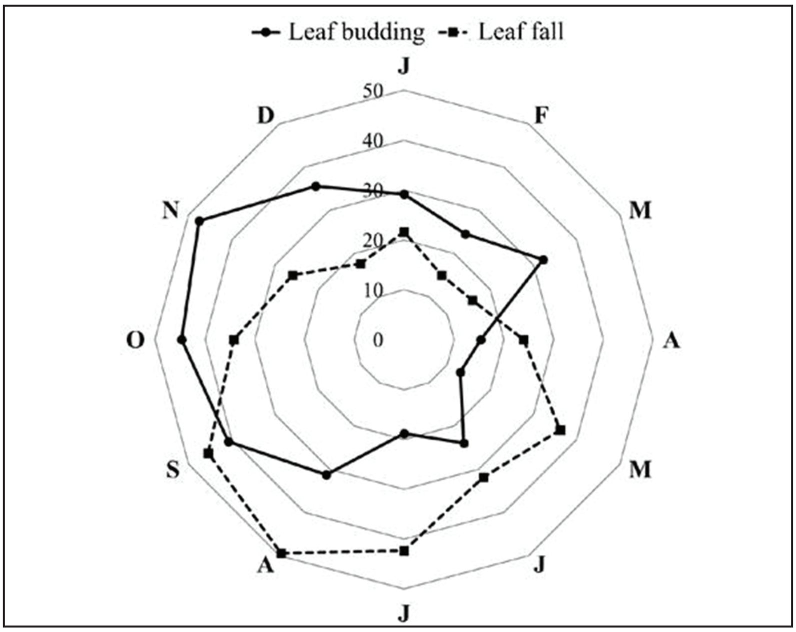

Figure 2 Intensity index (%) of leaf budding and leaf fall of sampled leaves for five forest types evaluated, where each letter refers to a month

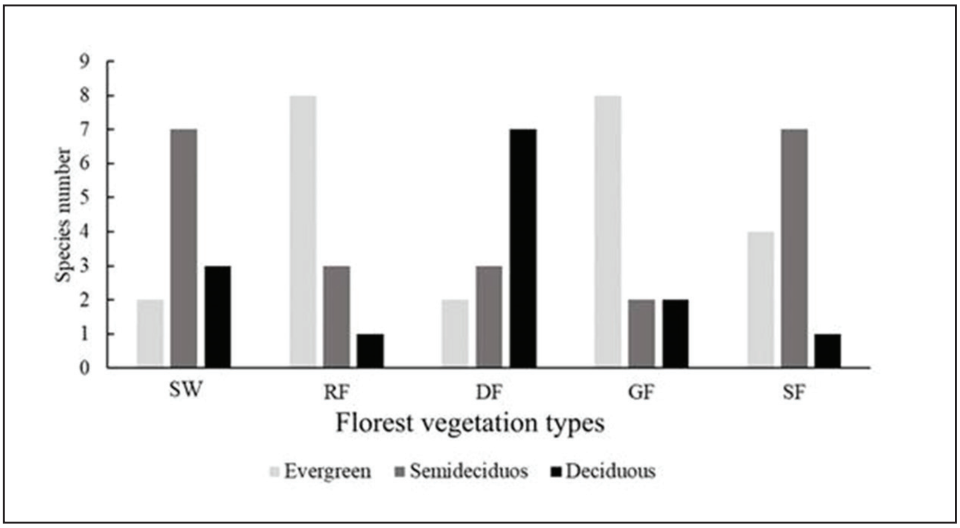

Figure 3 Classification of species according to leaf fall pattern in each forest vegetation type in the southwest of the Goiás state

SW = woody savanna, SF = semideciduous forest, DF = deciduous forest, RF = riparian forest, GF = gallery forest relative density was considered, the evergreen was the predominant phenology in woody savanna, semideciduous forest, flooded gallery forest and riparian forest vegetation types, while the semideciduous predominated in deciduous forest.

In general, leaf budding showed a seasonal pattern for all vegetation types, with lowest intensity occurs at the start of the dry season (April to July) and high intensity at the end of the dry season, continuing until the beginning of the rainy season (Figure 4-A). This is supported by the values of Rayleigh test (z) and vector r in deciduous forest, semideciduous forest, woody savanna and flooded gallery forest (z = 87.4; 64.4; 50.4; 19.3 [P < 0.001 for all]; and vector r = 0.36; 0.30; 0.30; 0.16, respectively). Except for the flooded gallery forest, the leaf budding decreased in all vegetation types during the dry season. Deciduous forest showed the greatest variations in leaf budding intensity throughout the year among vegetation types (Figure 4-A). Nevertheless, riparian forest had the leaf budding better distributed throughout the year, indicating seasonality less pronounced than in other forests, as shown in the Rayleigh test (z = 4.8; P = 0.008).

Leaf falls also showed notable differences across all types of vegetation, and, in general, the greatest deciduousness occurred in the months with the lowest rainfall (Figure 4-B). Woody savanna (z = 22.8; P < 0.001; r = 0.37), semideciduous forest (z = 54.4, P < 0.001; r = 0.31) and riparian forest (z = 31.6; P < 0.001; r = 0.19) had seasonality with peak leaf fall in August. Deciduous forest had a peak related to the month of June, the beginning of the dry period (z = 96.5; P < 0.001; r = 0.37). However, flooded gallery forest had a more uniform distribution throughout the year when compared to other forests, although with greater leaf fall in August (z = 16.2; P < 0.001; r = 0.14). During the rainy season, all physiognomies reduced leaf fall.

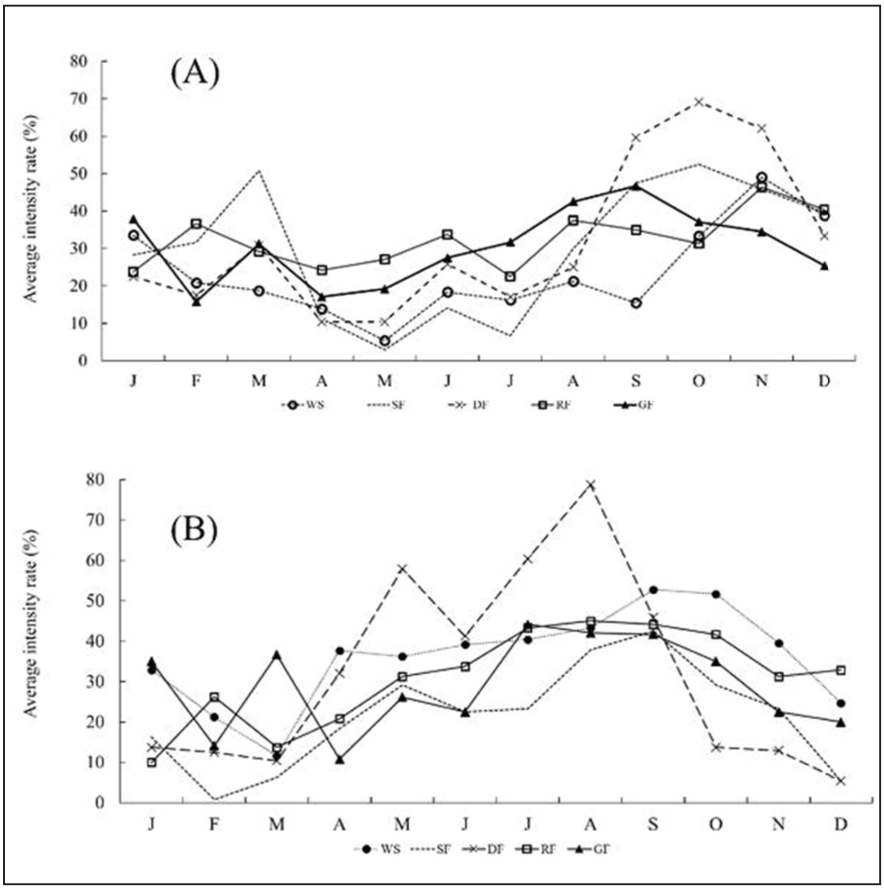

Figure 4 Intensity index (%) of leaf budding (A) and leaf fall (B) phenophases throughout one year, in five forest vegetation types studied in the southwest of the Goiás state

SW = woody savanna, SF = semideciduous forest, DF = deciduous forest, RF = riparian forest, GF = gallery forest

DISCUSSION

General phenological patterns in Cerrado vegetation type

There was a predominance of leaf maintenance (perennial) for the 53 species assessed, and also in the average relative density. However, the species number and the average relative density that predominated in each phenophase differed among vegetation types. The both vegetative phenophases peak were different among vegetation types, showing that the timing and intensity of events vary throughout the year. This may indicate a diversified resource available for herbivores and other organisms associated with these species over the year.

Studies involving species and woody communities in the Cerrado show that the peaks of several phenophases are linked to the end of the dry and the beginning of the rainy periods (Batalha & Martins 2004, Oliveira 2008, Pirani et al. 2009). This pattern was noted in our study, where leaf fall and leaf budding peaks happened in the end of the dry (August–September) and in in beginning of the rain seasons (October–November), respectively. However, this behaviour is not observed in other tropical forests, such as in the coastal regions of the Atlantic Forest (Morellato et al. 2000, Reich 1995) and the Amazonian Forest (Huete et al. 2006). The main cause of increased leaf fall at the end of the dry season in tropical forests is water stress. In order that woody plants do not lose water through evapotranspiration before the rainy season, trees drop their leaves (Reich & Borchert 1984). These present evergreen behaviour throughout the year, as they are located in regions without pronounced and severe periods of drought, as occurs in the Cerrado, even though the areas studied are located in ecotonal zones between the Cerrado and Atlantic Forest biomes. Although the flora of some of the vegetation types studied is associated with the Atlantic Forest, as found in a recent study for the gallery forests of the region (Nascimento et al. 2022), the evident seasonality in the vegetative patterns of the forests studied suggests a strong effect of the climate of the region.

Vegetative phenology among forest vegetation types

Studies show that water restrictions imposed by seasonality are important factors that define the proportions of deciduous species (Bastos & Ferreira 2010, Silvério & Lenza 2010), both in the Cerrado and in other biomes marked by climatic seasonality. Besides the seasonality implicit in the forests of Cerrado, other factors interfere in the vegetative phenology. Therefore, besides the climatic seasonality, the soil type and the water table depth are important factors that determine the floristic composition, thereby influencing the different levels of leaf fall in these forests (Furley & Ratter 1988). Nevertheless, species shared among vegetation types may present distinct phenological patterns due to intrinsic characteristics, such as plasticity to inhabit different environments (Reich 1995, Reich & Borchert 1984). An example can be observed in *Cordiera sessilis*, which in our study was characterised as evergreen and semideciduous, in the semideciduous forest and deciduous forest, respectively. This species has been showing an evergreen deciduousness under canopy of non-disturbed forests (Lopes et al. 2014). Although both semideciduous and deciduous forests in our study were under the same seasonal regime, the water stress may differ between them due to the microvariations of the relief, thus maintaining the perennially of this species in the semideciduous forest. Another example of plasticity can be observed in *Allophylus edulis*, a semideciduous species, which in our study was found in riparian forest and semideciduous forest, where both forests are different in soil moisture and nutrient availability. The germination and seedlings of *A. edulis* tolerate a range of condition that range from well-drained to flooded environments (Duarte et al. 2020), which may justify the occurrence of this species in these two vegetation types.

Based on a small set of species that had the highest relative density in each vegetation type, our study shows that there are few species shared among them, since only seven of the 53 species occurred in two vegetation types at the same time, such as *Protium heptaphyllum* and *Tapirira guianensis*. Therefore, our study suggests that the predominant phenological strategies both in abundance and species richness seems to be maintained by unique floristic elements particular of each vegetation type. Thus, the environmental variations that drive the plasticity above mentioned, seems to driving a unique flora in each forest vegetation type, even when these are spatially close to each other (Prado Júnior et al. 2012). Finally, we suggest that the different phenological strategies are maintained by the ability of some species to overcome environmental filters on a small scale.

Our findings showed that the intensity of vegetative events differs throughout the year among vegetation types. A determinant factor for this would be the type of soil and its drainage, which even in close forests condition the existence of diverse communities with different proportion of deciduous species. This demonstrates that the frequency and intensity of leaf fall and leaf budding can vary within the same forest remnant. For example, in May, a month of great water scarcity, the peak intensity of leaf budding in most vegetation types did not exceed 10%, while in the riparian forest it reaches 30%. Such a characteristic would have an important implication for the availability of resources for herbivorous insects, where species dependent on the rhythm of leaf production could find resources in different stretches of forest remnants throughout the year (Reich 1995). The vegetation type that reaches the leaf budding peaks in specific periods may characterise refugia for fauna during resource scarcity in other forest patches. Furthermore, herbivores with seasonal behaviour could, regardless of the time of year, find resources through the remnant.

As expected, deciduous forest showed more pronounced phenological differences, i.e., the highest number of deciduous species among the forest vegetation types. This probably is related to the shallow and well drained soils of the slope, where deciduous forest occurs. This provides the occurrence of typically deciduous species, and these patterns have also been recorded in other studies conducted in deciduous forest, with a sharp increase in leaf fall during the dry season (Andreis et al. 2005, Nunes et al. 2005). Even with its occurrence in more hydromorphic soils, during the drought the flooded gallery forest also showed an increase in leaf fall, probably in response to water stress in the period. As has been proposed the leaf fall is associated with intrinsic factors of the plants, but water stress would accelerate leaf fall or leaf budding (Reich & Borchert 1984). In other words, leaf fall in flooded gallery forest could also be related to the species behaviour, which even in moist soil lose more leaves in the dry season (Borchert 1994), suggesting that microclimatic conditions could influence leaf loss. For instance, the water evaporation from the moist soil is maintained throughout the year and elevates the relative humidity of the air in these humid forests (Furley & Ratter 1988), making their composition with few deciduous woody species. In this sense, small environmental variations such as relative humidity, make the floristic composition dissimilar (Prado Júnior et al. 2012), even in close forest environments and, in the case of the vegetation types studied, the composition of deciduous, semideciduous and evergreen species changes at short distances.

Finally, increase in leaf fall and reduction in leaf budding in the dry season had an almost inversely proportional pattern in all the vegetation types, although with different intensity responses, which may have the soil type as the main cause. The environmental heterogeneity inherent to the physico-chemical aspects and soil moisture between vegetation types can vary greatly, making the floristic composition peculiar and providing different phenological strategies along forest patches. Even though the general patterns for both phenophases tend to be similar, the intensity peaks at budding and deciduousness indicate that the vegetation types have their peculiarities, suggesting that the adjustment communities depend on the environmental gradient and floristic identity of each of them.

CONCLUSION

The phenophases showed marked seasonality (dry vs. rainy period), indicating a strong influence of the regional macroclimate on vegetative phenology in Cerrado forest patches. However, the phenology intensity was different among all vegetation types, indicating that fine-scale variations trigger vegetative phenology throughout the year. This could imply different resource supply along the forest patches, helping to maintain associated fauna (e.g., herbivores). Our study reinforces that the variety of ecosystems can provide resources for the fauna associated with it at different times of the year, with positive consequences on the conservation of plant-animal interactions. Therefore, the study confirms the importance of maintaining natural ecosystems remnants with a greater variety of vegetation types, plant diversity and environmental heterogeneity for the conservation and management of the Cerrado.

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