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ORIGINAL ARTICLE

Soil water availability and climate drive leaf demography of woody plants in the Brazilian savanna

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- **Background and Aims** Understanding the synergistic interactions between soil moisture and climate variability in leaf demography is critical to better understand how environmental conditions influence leaf production, senescence and turnover, and consequently plant productivity. We aimed to quantify leaf demography (longevity, survivorship and age structure) of nine savanna tree species with different leaf habits (three evergreen species, three semi-deciduous species and three deciduous species) and to investigate the effects of environmental predictors (soil water availability, precipitation, temperature and vapour pressure deficit) on leaf dynamics.
- **Methods** We conducted monthly surveys of leaf production, abscission, longevity and age over a 33-month period in the Cerrado biome. We used generalized linear models to evaluate the importance of soil moisture and climatic conditions on leaf dynamics.
- **Key Results** Evergreen species had the longest leaf longevity (20–26 months), followed by semi-deciduous (16–22 months) and deciduous species (12–13 months). The leaf age for 50 % survival probability was 12 months for deciduous species and 18 months for evergreen and semi-deciduous species. Although leaf abscission in the evergreen species occurred throughout the year, it was more concentrated at the end of the dry season. Leaf production peaked at the beginning of the rainy season across all three groups, despite a large variability among species within each group. Leaf longevity was strongly influenced by soil moisture at different depths.
- **Conclusion** Our results indicate that woody plants in the Cerrado have species-specific adaptations to climate seasonality and soil water availability, with leaf dynamics varying according to the degree of deciduousness. Environmental factors exert a stronger influence on deciduous and semi-deciduous species than on evergreen species. We highlight that recent and projected increases in temperature and declines in precipitation may compromise carbon assimilation by woody plants in the Cerrado, with potential consequences for ecosystem productivity.

Key words: Climatic seasonality, hydraulic shortcut, leaf deciduousness, leaf longevity, vegetative phenology.

INTRODUCTION

The structure and functioning of savanna vegetation are highly influenced by seasonal climate, with soil water availability as a critical factor affecting ecosystem processes, such as net primary productivity and nutrient cycling (Lehmann *et al.*, 2014; Dahlin *et al.*, 2017; Lira-Martins *et al.*, 2022). The Cerrado, the world's most diverse savanna (Murphy *et al.*, 2016), experiences significant rainfall seasonality (Oliveira-Filho and Ratter, 2002; Silva *et al.*, 2008), which leads to water restrictions on vegetation during the dry season (Franco, 2002; Oliveira *et al.*, 2005; Silva *et al.*, 2008; Butler *et al.*, 2012). In recent years, the Cerrado has undergone rapid land-use changes, leading to increasingly dry and hot conditions owing to the replacement of native vegetation by pastures and crops (Klink *et al.*, 2020; Hofmann *et al.*, 2021; Rodrigues *et al.*, 2022).

Woody savanna species display varying degrees of leaf deciduousness, representing different adaptive strategies for coping with seasonal water stress, nutrient allocation, carbon assimilation and use (Lenza and Klink, 2006; Oliveira, 2008). Several studies have highlighted the importance of understanding these adaptive strategies in the context of climatic seasonality to better understand the functioning of savanna vegetation (Rossatto *et al.*, 2013; Bueno *et al.*, 2018; Cure *et al.*, 2023). This information is useful for determining the consequences of rising temperatures and reduced rainfall throughout the Cerrado biome (Hofmann *et al.*, 2021) on carbon assimilation by plants with different leaf habits or degrees of deciduousness.

Classifying woody plants from the Cerrado into functional groups based on their vegetative phenological behaviour is common (Lenza and Klink, 2006; Goldstein *et al.*, 2008; Pirani *et al.*, 2009; Silvério and Lenza, 2010). The leaf habits of woody plants in the Cerrado vary widely, from evergreen species to completely deciduous species (Franco *et al.*, 2005; Lenza and Klink, 2006). However, our understanding of the vegetative phenology of savanna woody species in the Cerrado is mainly derived from qualitative or semi-quantitative data (Bucci *et al.*, 2005; Damascos *et al.*, 2005; Souza *et al.*, 2009). Little is known about leaf dynamics, longevity or the influence of environmental factors on leaf production and abscission control. Although plant phenological behaviour and leaf longevity are not necessarily directly related, they contribute to determining the level of leaf deciduousness, making the definition of phenological groups complex and somewhat ambiguous (Engelbrecht and Kursar, 2003). Most previous studies investigating the phenological adjustment of species to local environmental variations have considered the individual as the sampling unit, and little is known about leaf dynamics and longevity in savanna woody species.

Leaf longevity is a key functional trait influencing plant nutrient synthesis, recycling and overall ecosystem nutrient dynamics (Chabot and Hicks, 1982; Kikuzawa, 1991; Kikuzawa and Lechowicz, 2011). Understanding the determinants of interspecific variation in leaf longevity is fundamental to evaluating the contrasting strategies of conservation and acquisition of nutrients and water use by coexisting savanna species under strong environmental filters (Maracahipes *et al.*, 2018; Power *et al.*, 2019; Carrijo *et al.*, 2021). These distinct resource-use strategies can shape the timing of leaf flushing and abscission, thereby influencing the lifespan of leaves in species with different phenological behaviours. Interspecific variations in leaf longevity, despite the level of deciduousness, could reveal more accurately how different woody plants cope with the chronic limitations of nutrients and water characteristic of Brazilian savanna soils (Haridasan, 2008; Lira-Martins *et al.*, 2022). Consequently, examining the relationships between leaf longevity, soil water and and nutrient availability may help elucidate how climate variability affects nutrient cycling in Cerrado plant communities, a topic still poorly investigated for tropical savannas. Understanding these linkages between climate, soil water availability and leaf demography can reveal key ecological mechanisms underlying water and carbon assimilation, and ultimately, the carbon stocks of Cerrado woody vegetation (Arantes *et al.*, 2016; Sankaran, 2019).

In this context, our study is unique in directly measuring, rather than merely estimating, the leaf longevity and age of woody species in the Cerrado, and in linking leaf demographic events to local climate and the temporal dynamics of water availability for plants. We raised two key questions: (1) How do the dynamics and seasonality of leaf phenological events such as production, abscission, leaf longevity, age and survivorship curves differ among woody species with different degrees of deciduousness in the Cerrado (Fig. 1A)? (2) How does soil water content and climatic seasonality influence leaf production and abscission in species with different levels of deciduousness (Fig. 1B)? We hypothesized that: (1) evergreen species produce longer-lasting leaves with higher survivorship probabilities and greater overlap between leaf development stages than semi-deciduous and deciduous species (Fig. 1A); and (2) environmental variables, such as precipitation, temperature, vapour pressure deficit (VPD) and soil water availability, would have a stronger influence on leaf production and abscission in species with more pronounced seasonal leaf dynamics (deciduous and semi-deciduous) than in those with less seasonal leaf dynamics (evergreen) (Fig. 1B).

MATERIALS AND METHODS

Study site

The field study was conducted in the IBGE Ecological Reserve (RECOR) in Brasília, Federal District, Brazil (15°55′S, 47°51′ W) (Fig. 2). RECOR comprises an area of 1300 ha, and the predominant vegetation is woody savanna (locally known as *cerrado típico*) (IBGE, 2004). The prevalent soil type is a well-drained Oxysol (red-yellow latosol), with an altitude between 1045 and 1146 m (IBGE, 2004). The climate is seasonal (dry season between April and September and wet season between October and March; Fig. 3).

Environmental variables

During the field study (2001–2003), we obtained the following climate variables from the Ecological Station of RECOR, located approximately 1.5 km from the study area: luminosity (number of sunshine hours), precipitation, minimum air temperature, average air temperature, maximum air temperature and relative air humidity. Air temperature and relative air humidity were used to calculate VPD (Rundel and Jarrel, 1989). From October 2001 to September 2002 (except February), soil moisture was measured at three depths (up to 100 cm, between 100 and 200 cm, and between 200 and 300 cm). Soil water was measured using time-domain reflectometry (TDR) as described by Silva (2003). We estimated soil moisture in February 2002 as the average between January and March of the same year (Fig. 3).

Leaf phenological event monitoring

We tracked leaf production and shedding for nine woody species over 33 months, categorizing them into three phenological categories, simplifying the definitions of Lenza and Klink (2006) and Franco *et al.* (2005): evergreen (EVE) [*Miconia albicans* (Sw.) Triana, *Miconia fallax* DC. and *Myrsine guianensis* (Aubl.) Kuntze]; semi-deciduous (SEM) [*Ouratea hexasperma* (A.St.-Hil.) Baill., *Roupala montana* Aubl. and *Styrax ferrugineus* Nees & Mart.]; and deciduous (DEC) [*Blepharocalyx salicifolius* (Kunth) O.Berg, *Byrsonima verbascifolia* (L.) DC. and *Kielmeyera coriacea* Mart. & Zucc.]. These species are widely distributed in savannas of the Brazilian central plateau (Felfili and Silva Júnior, 1993; Santos *et al.*, 2012) and are representative of the different phenological behaviours

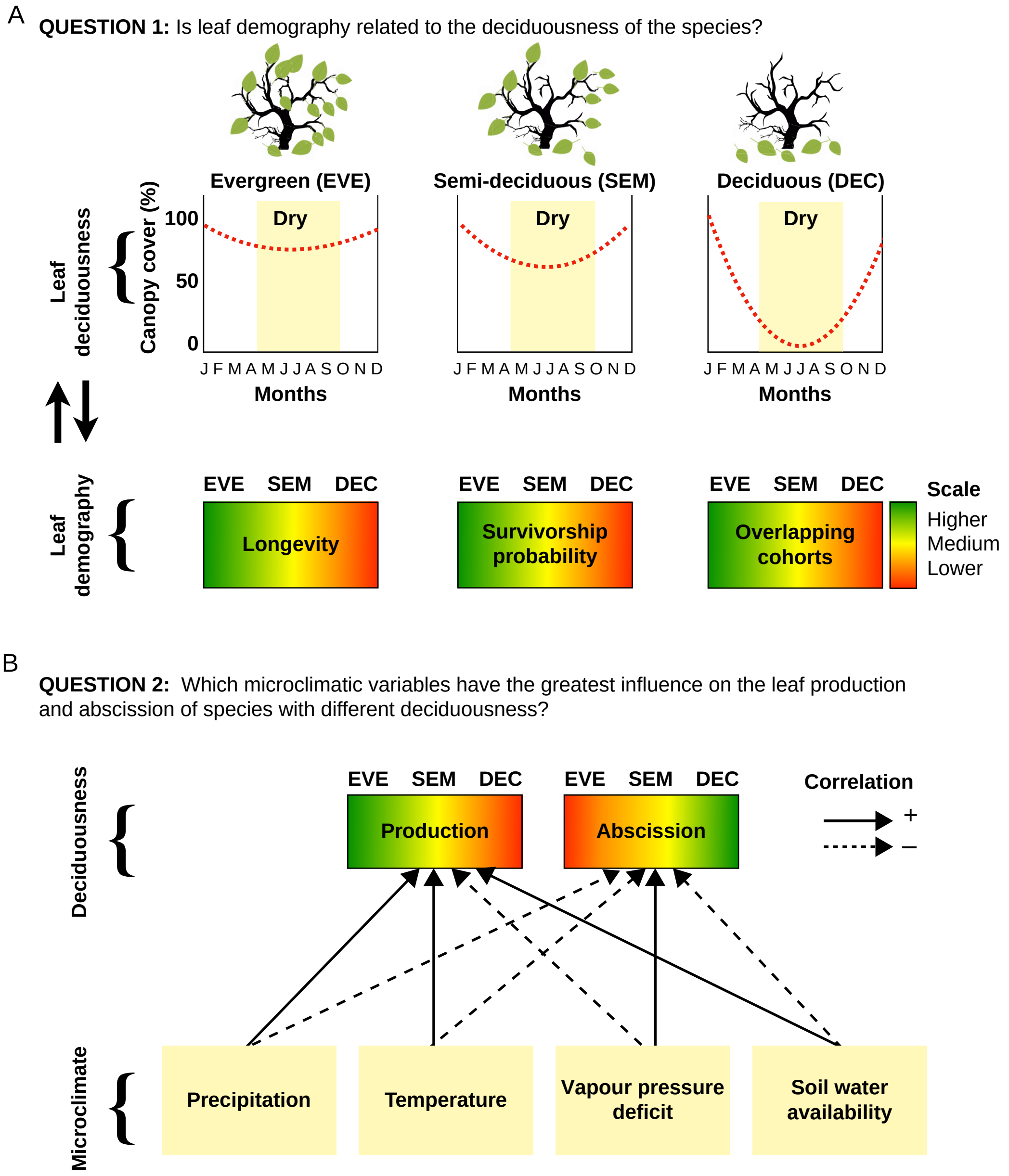

Fig. 1. Schematic framework showing the expected leaf dynamics and demography (hypothesis 1) with different levels of leaf deciduousness (A), and the relationships between environmental variables and leaf events (hypothesis 2) of Cerrado woody species with different levels of leaf deciduousness (adapted from Lenza and Klink 2006) in the IBGE Ecological Reserve in Central Brazil. EVE = evergreen; SEM = semi-deciduous; DEC = deciduous. (B) Expected effects of the environment on the leaf demography of Cerrado woody species with different leaf habits.

of woody plants in the savanna formations of the biome (Lenza and Klink, 2006).

We monthly evaluated leaf phenological events in 10 adult individuals of each species (except *Miconia fallax*, which had six individuals) from March 2001 to November 2003 (33 months), encompassing three complete dry periods, two complete rainy periods and two incomplete rainy periods. We marked three terminal branches of each individual with numbered aluminium tags. The leaves of all branches were marked with coloured strips and numbered in an increasing sequence from the base to the apex of the branch (Supplementary Data Fig. S1). Branches that lost all leaves during the dry period and remained alive were tagged until new leaves were produced. Eventually, dead or broken branches were replaced by new tagging on the same plant to maintain three branches per individual throughout the study period.

To determine leaf longevity for all studied species, we recorded the number of leaves that fell (leaf abscission) and new leaves produced on the branches (leaf production) in each monthly census. Each event was identified and numbered using previously described criteria. In total, we recorded 4039 leaf abscissions and 3852 leaf production events. The intermediate date between consecutive measurements was considered to determine the time of leaf production and fall. We determined the longevity of 3547 leaves from production to abscission. We classified all leaves into three developmental stages: (1) young leaves, (2) mature leaves and (3) senescent leaves (for details, see Supplementary Data).

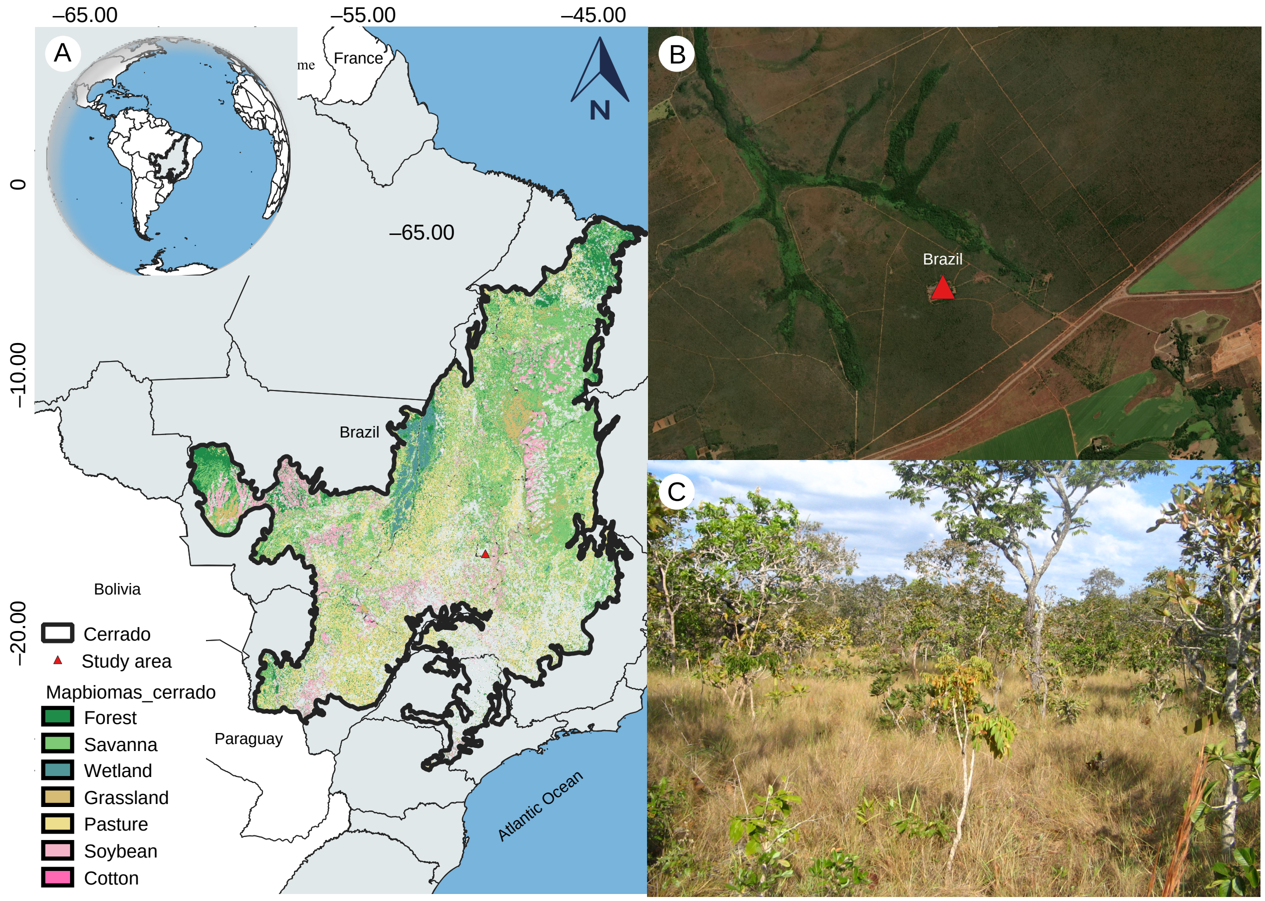

FIG. 2. Location of the study site in the IBGE Ecological Reserve, Central Brazil (from: MapBiomas - https://mapbiomas.org).

Data analysis

For the dynamics of leaf activity over time, we produced time-series graphs displaying the total count of leaves as well as the number produced and shed during each census period. We examined the seasonality of leaf production and abscission events for each species using circular distribution analysis, as outlined by Zar (2010). This involved computing the average occurrence (peak) angle for each event and the circular dispersion around this angle and assessing the uniformity of these events across the year using Rayleigh's test. For these circular analyses, we only included data spanning the first 24 months of our study (October 2001 to September 2003), which allowed us to monitor phenological events across two annual cycles. For these circular analyses, we used the R package 'circular' (Agostinelli and Lund, 2023).

Leaf longevity across species was compared using Kruskal–Wallis tests. When significant differences were found, we conducted further analyses using non-parametric multiple comparisons, implemented with the 'kruskalmc' function in the R package 'pgirmess'. Despite various transformations, leaf longevity data did not conform to the assumptions required for parametric testing.

Leaf age class was assessed based on three developmental stages: young, mature and senescent. Life table analyses were performed separately for each of the nine species and the three phenological groups based on leaf age measured in months. Leaf age comparisons between species and survivorship curves between phenological groups were also conducted using the Kruskal–Wallis test and the 'survdiff' function from the R package 'survival' (Therneau, 2024), respectively, utilizing a chi-squared approximation.

To investigate the effects of environmental conditions on leaf dynamics, the original field data were reanalysed by employing a linear mixed model (LMM). The response variables in this model were leaf production and abscission. The predictors included phenological group, luminosity, precipitation, minimum air temperature, average air temperature, maximum air temperature, relative air humidity, VPD and soil moisture at three different depths (up to 100 cm, between 100 and 200 cm, and between 200 and 300 cm). We utilized the 'lmer' function from the 'lme4' package (Bates *et al.*, 2015). For this analysis, we selected the most parsimonious models based on their lowest Akaike information criterion (AIC) values, as detailed in Supplementary Data Tables S6 and S7. We also evaluated residual diagnostics for these selected models (Figs S2–S4).

All analyses were conducted using R statistical program (R Core Team, 2024), with a predetermined significance level of 5 % ($\alpha = 0.05$) applied to all tests.

RESULTS

Climate and soil water

Our study showed clear seasonal patterns for both climate and soil water availability for the studied period. The rainy season,

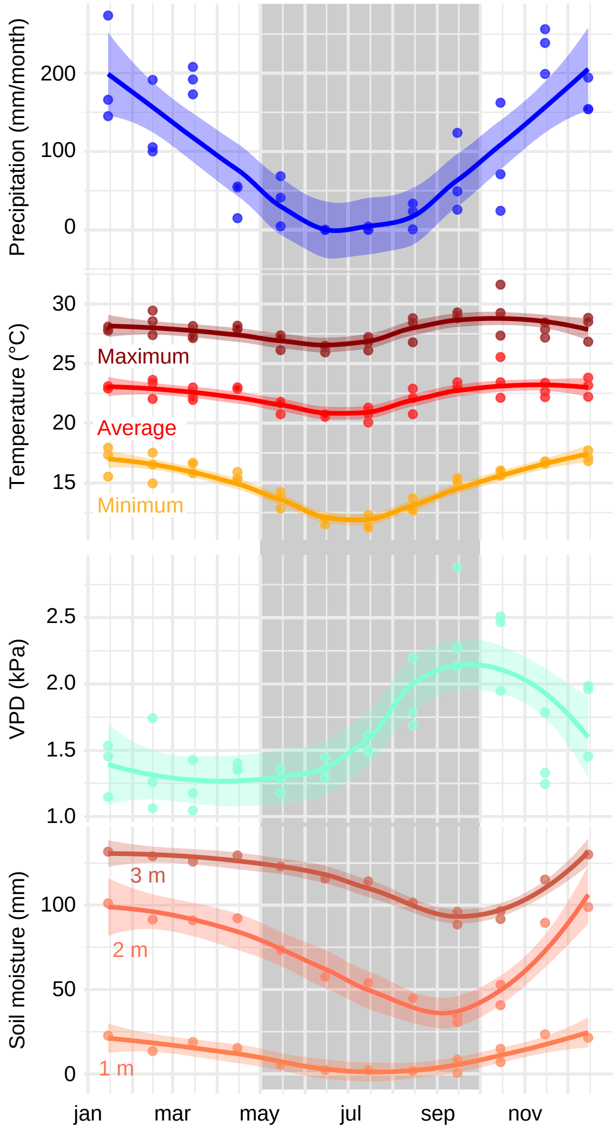

FIG. 3. Climate and soil moisture in a savanna in the IBGE Ecological Reserve, Central Brazil. The grey area in the plot represents the dry season (May to September). We used monthly climate information from January 2001 to December 2003, except for soil moisture, which ranged from October 2001 to September 2002.

characterized by higher temperatures, spans from October to March, followed by the dry season, characterized by lower temperatures from May to August. Short transition periods between the two seasons occur in April and September. Highest maximum, average and minimum air temperatures were observed during the rainy season, whereas the lowest values were recorded during the middle of the dry season, specifically in June and July. Notably, the minimum air temperature exhibited more pronounced seasonality. VPD also showed marked seasonal variation, with higher values during the transition between the dry and rainy seasons and lower values towards the end of the rainy season and the beginning of the dry season (Fig. 3).

Seasonal variations in soil water availability for plants were observed at all three soil depths, with the most significant variations occurring in the two deeper layers, mainly between 1 and 2 m (Fig. 3). The lowest water availability values were recorded in the topsoil throughout the year compared with the other soil layers, which consistently remained below 40 mm and approached zero during the dry peak period (May–August). The lowest water availability in the top layer (0.5–1 m) was recorded in September and October (Fig. 3). These results indicate higher water stress during the dry period, mainly between May and September, with reduced water availability up to 3 m depth and greater evaporative air demand, as inferred from VPD. However, plant water stress decreased from November to May due to higher rainfall, increased soil moisture and reduced evaporative demand (Fig. 3).

Leaf dynamics

Leaf dynamics varied among species of different phenology groups and, in some cases, among species of the same phenology group (Fig. 4; Supplementary Data Fig. S2). Leaf production for two of the evergreen species (*Miconia albicans* and *Miconia fallax*) was concentrated during the rainy season. However, leaf abscission occurred throughout the year. The number of leaves in both species fluctuated slightly, with higher numbers during the rainy season. For *Myrsine guianensis*, leaf dynamics consist of two annual events: leaf fall and production. Leaf abscission occurred between July and September, whereas leaf production occurred between October and November. This led to almost complete replacement of all leaves on the marked branches. A second and less evident leaf abscission event occurred in November and December, followed by leaf flush, which was not evident in December and January, resulting in a subtle reduction of leaves on the plants in the middle of the dry season (Fig. 4).

The three semi-deciduous species (*O. hexasperma*, *R. montana* and *S. ferrugineus*) exhibited a clear seasonal leaf abscission, with peak at the end of the dry season and leaf production concentrated during the transition between the dry and rainy periods (September and October). This asynchrony between abscission and production led to the exchange of almost all the leaves in the canopy at the end of the dry season. Caterpillars of *Eustema opaca* (Notodontidae) consumed most of the leaves produced by *R. montana* in September and October 2001, resulting in a significant decrease in the number of leaves. However, two new cohorts of leaves were produced between December 2001 and April 2002, which restored the canopy of *R. montana* studied individuals (Supplementary Data Fig. S5).

For deciduous species (*Blepharocalyx salicifolius*, *Byrsonima verbascifolia* and *K. coriacea*), leaf abscission started at the end of the rainy season and lasted throughout the dry period, with an intense reduction in leaves in the population in July and August. The intense leaf production in September resulted in rapid foliage recovery in October. However, in *K. coriacea*, the greater asynchrony between abscission and production means that the complete absence of leaves in the plants is longer than that in the other two deciduous species (Fig. 4; Supplementary Data Fig. S5).

Leaf abscission and production showed a seasonal pattern ($P < 0.05$) across all nine studied species. However, these phenological events were less concentrated in evergreen species (lower r values) and more concentrated in deciduous species (Supplementary Data Tables S1 and S2). Leaf abscission in evergreen species occurred throughout the year, whereas leaf production peaked during the rainy season. In contrast, deciduous species showed both leaf production and abscission concentrated in the dry season, with

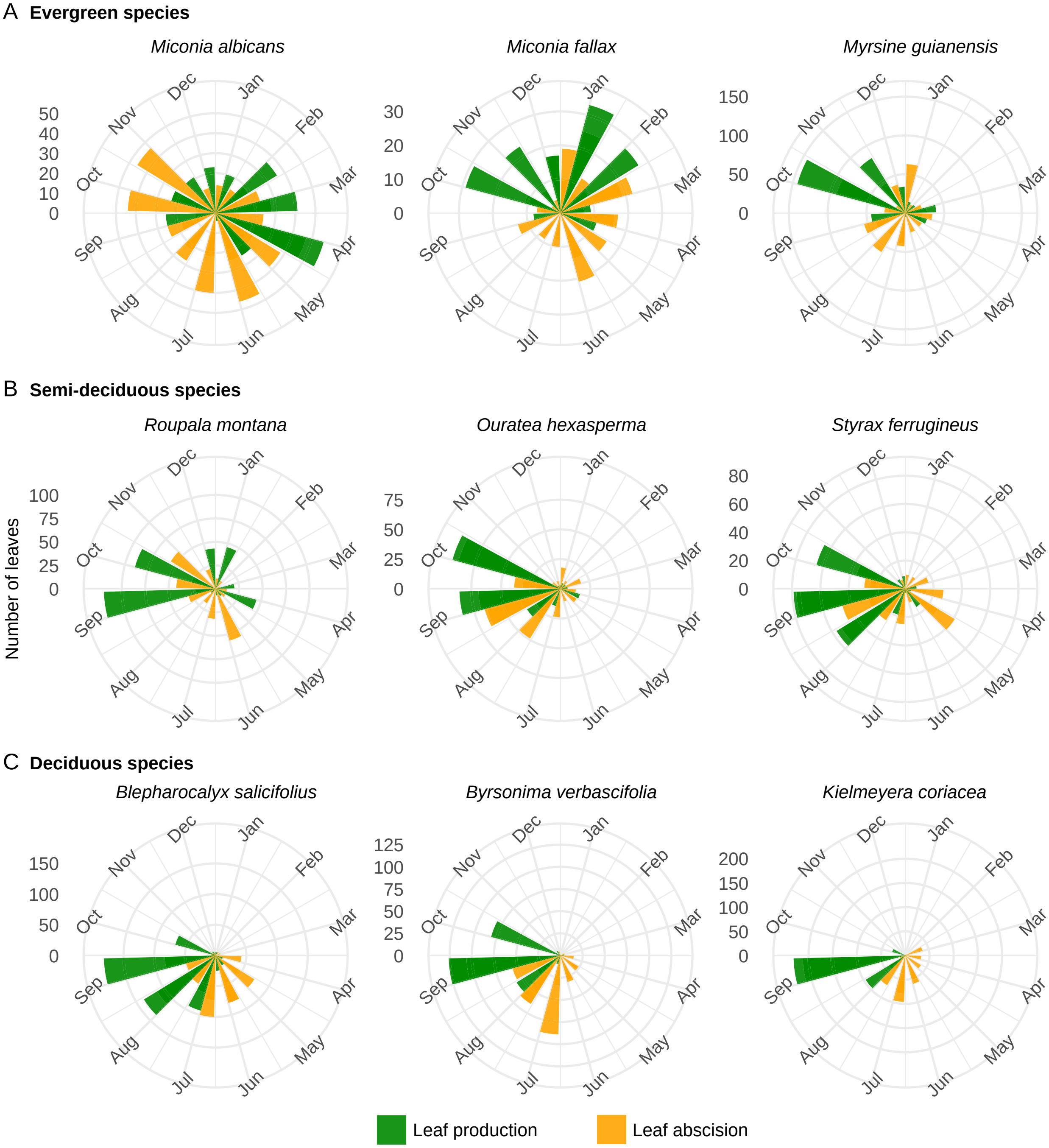

Fig. 4. Circular histograms depicting the production of abscission leaves of evergreen (A), semi-deciduous (B) and deciduous (C) species in a savanna woody species of the IBGE Ecological Reserve, Central Brazil.

abscission peaking early (June and July) and leaf production occurring later (August and September). Semi-deciduous species exhibited intermediate patterns, with leaf abscission from August to September, and leaf production from September to November (Tables S1 and S2).

Leaf longevity

Overall, evergreen and semi-deciduous species tended to have the longest leaf longevity (6.6–13.3 and 9–13.6 months, respectively) than deciduous species (9–9.6 months), although there was considerable variation within each group (Fig. 5A; Supplementary Data Table S3). We observed greater variability in leaf longevity among evergreen and semi-deciduous species than among deciduous species.

There were significant differences in leaf longevity between the species (Kruskal–Wallis, $\chi^2 8 = 934.79$; $P < 0.001$; Fig. 5B; Supplementary Data Table S3). *Roupala montana*, *Miconia albicans* and *Miconia fallax* had the longest average leaf longevity (13.6, 13.3 and 11.2 months, respectively), significantly longer than the other species. *Ouratea hexasperma*, *S. ferrugineus*, *Byrsonima verbascifolia*, *Blepharocalyx salicifolius* and

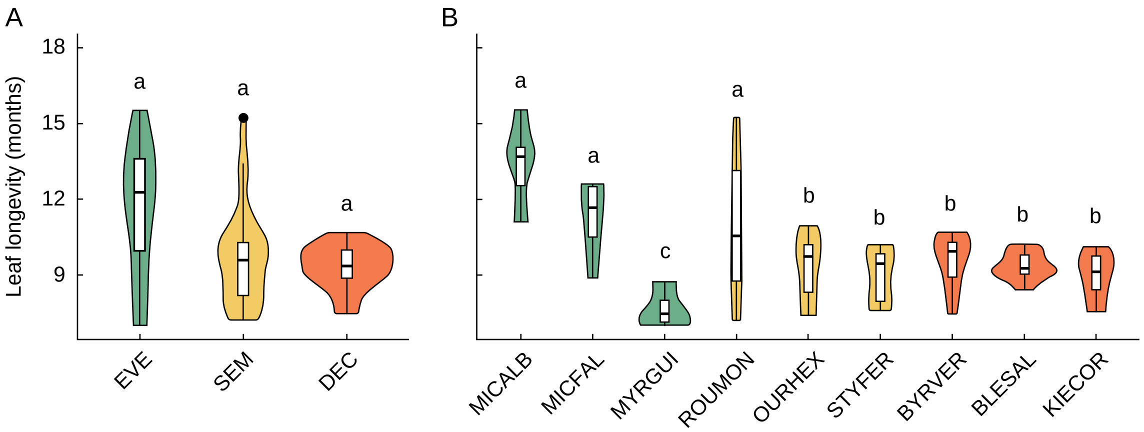

Fig. 5. Violin plots (boxplots combined with kernel density plots) showing leaf longevity of evergreen (green), semi-deciduous (yellow) and deciduous (orange) woody species in the savanna of the IBGE Ecological Reserve, Central Brazil. Boxplots show median, and 25th and 75th percentiles. Same lowercase letters represent similar longevity (Kruskal–Wallis test) between phenological groups (A) and between species (B). MICALB = *Miconia albicans*; MICFAL = *Miconia fallax*; MYRGUI = *Myrsine guianensis*; OURHEX = *Ouratea hexasperma*; ROUMON = *Roupala montana*; STYFER = *Styrax ferrugineus*; BYRVER = *Byrsonima verbascifolia*; BLESAL = *Blepharocalyx salicifolius*; KIECOR = *Kielmeyera coriacea*.

K. coriacea had similar leaf longevity (9–10 months). The average leaf longevity of *Myrsine guianensis* (6.6 months) was shorter than that of the other eight species (Fig. 5B; Table S3).

Leaf age structure

Leaf age confirms previous classification of the species into different phenological groups, but also reveals important temporal patterns in leaf ontogeny. Evergreen species were characterized by the overlapping of young, mature and senescent leaves throughout a specific year and by the presence of mature leaves throughout the entire study period (Fig. 6). In contrast, the deciduous species were characterized by a clear temporal shift between the leaf development ontogenetic stages. In these species, there was a high frequency of senescent leaves during the transition between the wet and dry seasons (mainly between March and May), young leaves at the end of the dry season (August to October) and mature leaves in the middle of the wet season (mainly from November to February) (Fig. 6). Finally, the semi-deciduous species showed a modest, though significant, alternation in the frequencies between the three stages of leaf development throughout the year, with a predominance of young leaves at the end of the dry period and beginning of the rainy period (September to December), mature leaves in the mid-rainy period (mainly from December to February), and senescent leaves at the end of the rainy and beginning of the dry season (mainly from March to June) (Fig. 6).

Leaf survival curves

Leaf survival did not differ between the evergreen and semi-deciduous species ($\chi^2 = 0$; df = 1; $P = 0.05$); however, these probabilities were greater than those of the deciduous and semi-deciduous species ($\chi^2 = 729$; df = 1; $P < 0.001$). In addition, leaf survival differed between the deciduous and evergreen groups ($\chi^2 = 706$; df = 1; $P < 0.001$) (Supplementary Data Fig. S6). Remarkably, at 12 months of age, the probability of leaf survival for deciduous species was 50 %, whereas in evergreen and semi-deciduous species, this occurred at 18 months of age (Fig. S6). Leaf survival probabilities also differed among some of the species within the same phenological groups (Fig. 7; Table S4).

Effects of climate and soil moisture on leaf dynamics

The effects of the environment (soil moisture and temperature) on leaf production for deciduous species differed from those of evergreen and semi-deciduous species, but not between species of the last two phenological groups (Supplementary Data Table S5; Fig. 8). The best-fit linear model for leaf production explained 48 % of the data variability ($F_{9,116} = 14.06$, $r^2_{\mathrm{adj}} = 0.48$). The highest leaf production occurred during periods with the lowest water availability in the soil between 1 and 2 m depth, with a stronger relationship for deciduous species (Fig. 8; Fig. S7). In general, leaf production increased with luminosity and minimum temperatures and with lower maximum temperatures. Again, these effects were stronger in deciduous species than in semi-deciduous and evergreen species (Fig. 8).

Regarding leaf abscission, the effect of the environment differed among the species of the three phenological groups (Supplementary Data Table S5). The best-fit linear model for leaf abscission explained 41 % of the variability in the data ($F_{9,116} = 15.43$; $r^2_{\mathrm{adj}} = 0.41$). The leaf abscission of the nine species was related to minimal temperatures and soil moisture at a depth of 1 m, being higher in periods of higher minimal temperatures and lower water availability (Fig. 8). The effects of soil water availability and minimum temperature were stronger in deciduous species than in semi-deciduous and evergreen species (Fig. 8). Precipitation was not an important climatic variable for explaining the variability in leaf production or abscission, and VPD contributed to explaining only leaf production (Tables S6 and S7).

DISCUSSION

General patterns

Our findings reveal distinct and previously unrecognized patterns in leaf demography that challenge the traditional

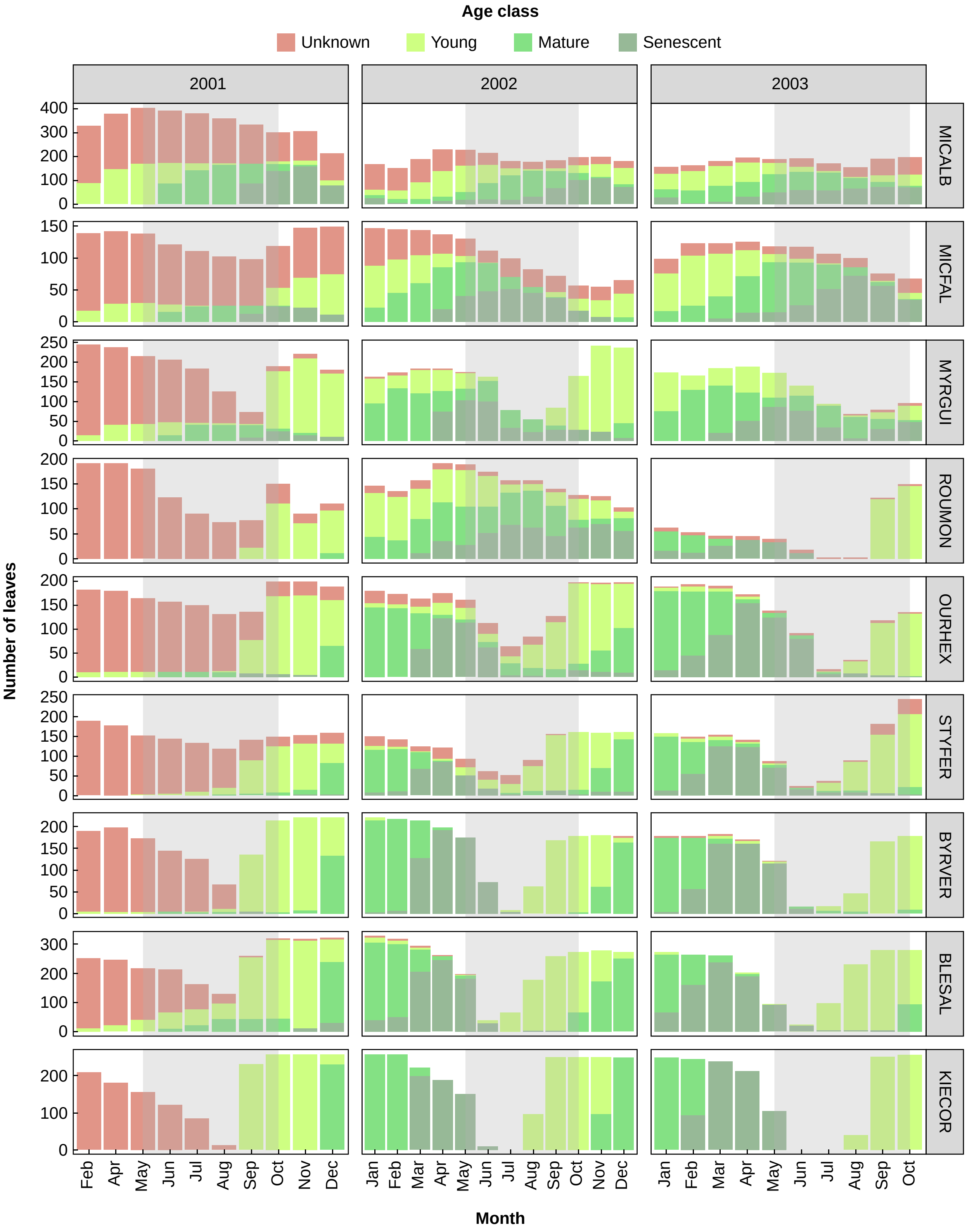

FIG. 6. Leaf age of woody species of different phenological groups in a savanna of the IBGE Ecological Reserve, Central Brazil. The grey area in the plot represents the dry season (May to September). MICALB = *Miconia albicans*; MICFAL = *Miconia fallax*; MYRGUI = *Myrsine guianensis*; OURHEX = *Ouratea hexasperma*; ROUMON = *Roupala montana*; STYFER = *Styrax ferrugineus*; BYRVER = *Byrsonima verbascifolia*; BLESAL = *Blepharocalyx salicifolius*; KIECOR = *Kielmeyera coriacea*.

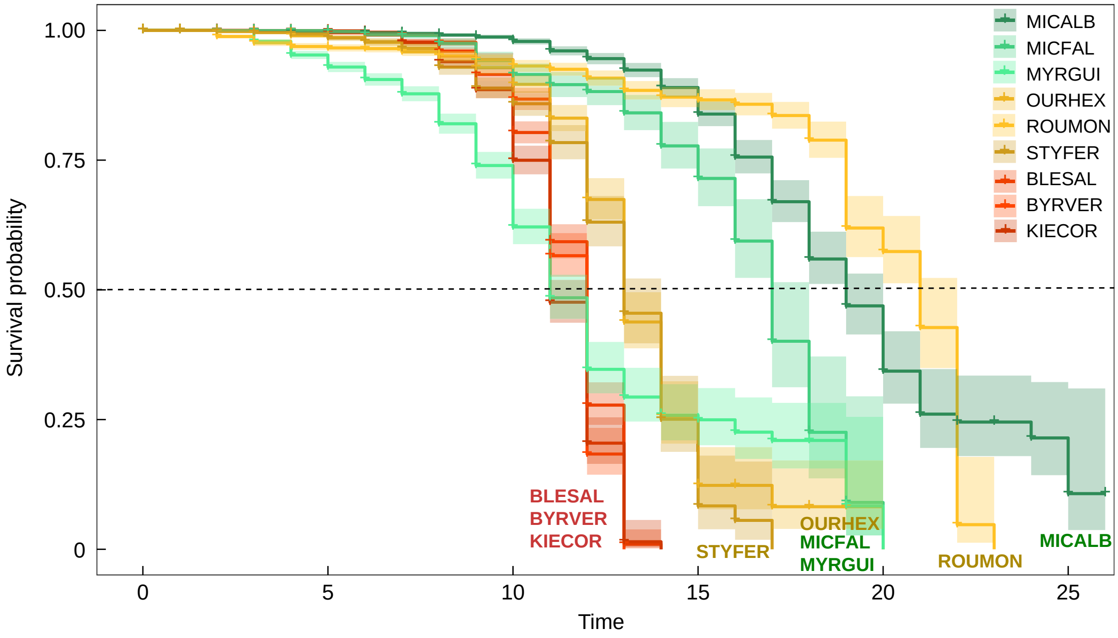

FIG. 7. Survival curves of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil, with different deciduousness levels: evergreen (green), semi-deciduous (yellow) and deciduous (orange). The dotted line indicates 50 % survival probability. MICALB = *Miconia albicans*; MICFAL = *Miconia fallax*; MYRGUI = *Myrsine guianensis*; OURHEX = *Ouratea hexasperma*; ROUMON = *Roupala montana*; STYFER = *Styrax ferrugineus*; BYRVER = *Byrsonima verbascifolia*; BLESAL = *Blepharocalyx salicifolius*; KIECOR = *Kielmeyera coriacea*.

classification of Cerrado woody species based solely on their degree of deciduousness. We demonstrate that leaf longevity provides a more integrative indicator of phenological strategies, as semi-deciduous species may retain long-lived leaves, whereas some evergreen species exhibit comparatively shorter leaf lifespans. These results indicate that leaf habit is not a fixed categorical trait, but rather a dynamic and context-dependent response to environmental variability. Consistent with our first hypothesis, evergreen species produced leaves with higher survival probabilities and greater longevity than semi-deciduous and deciduous species (Franco *et al.*, 2005; Lenza and Klink, 2006). Our second hypothesis was also supported, as seasonal climate and soil water availability exerted weaker effects on leaf abscission in evergreen species compared with the other phenological groups. Moreover, interspecific variation in leaf demography within the same phenological category highlights a high degree of phenotypic plasticity among Cerrado woody plants (Lenza and Klink, 2006; Silvério and Lenza, 2010).

Leaf dynamics

Our results confirmed the phenological patterns of foliage replacement during the late dry season for deciduous and semi-deciduous species, consistent with patterns widely reported for woody plants in seasonally climate dry savannas (Sarmiento *et al.*, 1985; Williams *et al.*, 1997; de Bie *et al.*, 1998; Guan *et al.*, 2014), and across different regions of the Cerrado biome (Mantovani and Pimenta, 1988; Miranda, 1995; Jackson *et al.*, 1999; Lenza and Klink, 2006; Oliveira, 2008; Pirani *et al.*, 2009). These species appear to rely on synchronized foliage exchange as a key strategy for coping with prolonged periods of soil water limitation. However, the notable presence of evergreen species in these environments indicates that deciduousness alone cannot fully explain the range of adaptive mechanisms that Cerrado woody plants employ to regulate water use and maintain physiological activity during the dry season.

We observed that leaf production in evergreen woody species occurred continuously throughout the year, consistent with patterns reported for other savanna ecosystems (Franco *et al.*, 2005; Lenza and Klink, 2006; Silvério and Lenza, 2010). The persistence of foliage during the dry season suggests that leaf deciduousness in this group is weakly influenced by local climatic and edaphic stressors. Deep rooting systems play a crucial role in maintaining water supply during the peak of the dry season in Brazilian savannas (Oliveira *et al.*, 2005), when evaporative demand is highest. Similar patterns have been reported in African savannas, where leaf production is positively associated with water availability in shallow soil layers and with regrowth preceding the onset of the rainy season (Seghieri *et al.*, 2009; Guan *et al.*, 2014). Although semi-deciduous and deciduous species typically drop their leaves during the dry season, they also produce new cohorts of leaves during the driest months, indicating an ability to maintain water uptake even under pronounced seasonal deficits (Lenza and Klink, 2006; Silvério and Lenza, 2010). The considerable capacity of Cerrado woody species to store non-structural carbon reserves (Hoffmann *et al.*, 2004; Rocha *et al.*, 2025), combined with hydraulic redistribution that transfers water from deeper to shallower soil layers during drought (Scholz *et al.*, 2002; Oliveira *et al.*, 2005; Lira-Martins *et al.*, 2022), probably contributes to sustaining photosynthesis activity in evergreen species and supporting leaf production in more deciduous taxa when rainfall is absent.

Leaf abscission in evergreen species was not induced by seasonal water restriction, as indicated by the weak association between leaf loss and climate variables. This pattern suggests that evergreen Cerrado species possess physiological traits that buffer them against seasonal declines in soil water availability.

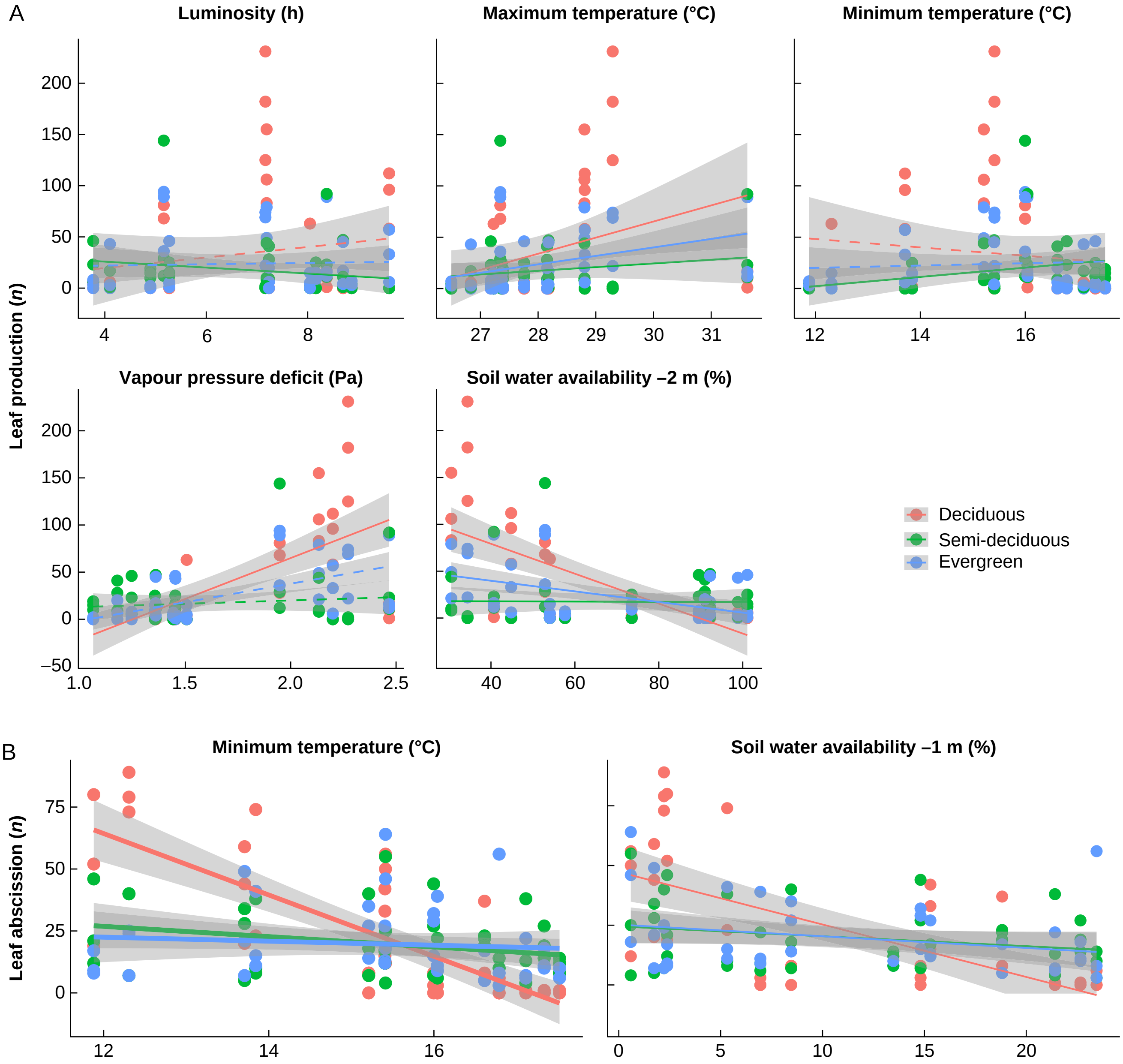

FIG. 8. Effect of climate and soil moisture on leaf production (A) and leaf abscission (B) in different phenological groups (DEC = deciduous, EVE = evergreen and SEM = semi-deciduous) in a savanna of the IBGE Ecological Reserve, Central Brazil. The graphs show only the variables selected as the best models (see Supplementary Data Tables S6 and S7). Solid lines indicate significant relationships, whereas dashed lines represent non-significant relationships.

One likely mechanism is their substantial capacity to store non-structural carbohydrates (NSCs) in below-ground organs. High concentrations of root carbohydrate reserves, characteristic of evergreen savanna species (Hoffmann *et al.*, 2004), enable them to maintain leaf hydraulic function and metabolic activity throughout the dry season, reducing the need to shed leaves as a drought-avoidance strategy.

Leaf longevity and survival

Our results indicate that leaf longevity may be a more reliable indicator of the phenological behaviour of woody Cerrado species than deciduousness alone. We observed clear differences in the leaf survival curves among deciduous, semi-deciduous and evergreen species. Deciduous species showed leaf survival rates below 50 % after 1 year, whereas semi-deciduous and evergreen species exhibited survival probabilities of 50 % after approximately 1.5 years. For example, *Myrsine guianensis* has been previously classified as evergreen (Franco *et al.*, 2005; Lenza and Klink, 2006), exhibited biannual leaf abscission and production, yet maintained a high maximum longevity, allowing it to sustain foliage throughout the year despite the short duration of the leaves produced. We also recorded higher maximum leaf longevity for evergreen species than for semi-deciduous and deciduous species, which is consistent with

Franco *et al*. (2005). For example, *R. montana*, previously classified as semi-deciduous, demonstrated similar or greater leaf longevity than some evergreen species, which could justify its reclassification as an evergreen. Therefore, determining the level of deciduousness of Cerrado woody species should consider not only the synchrony between leaf fall and leaf production (Lenza and Klink, 2006; Silvério and Lenza, 2010) but also the maximum leaf longevity and survival probabilities.

Phenological studies using similar methodologies for Cerrado woody plants have classified the same species which exhibit distinct phenological behaviours. These variations may have resulted from phenotypic plasticity in terms of leaf longevity. Consequently, leaf longevity may be a better indicator of phenological behaviour than simply measuring the degree of deciduousness, providing a more accurate understanding of photosynthetic activity, water and nutrient use in relation to climatic seasonality. This does not undermine the value of classical phenological studies, which are useful for classifying the degree of deciduousness within communities and for understanding the relationship between soil water and plant leaf dynamics. However, more accurate analyses of plant behaviour in response to seasonal soil water availability in the Cerrado require quantitative studies of leaf dynamics, including leaf longevity (e.g. previous studies) and leaf age (present study). Leaf longevity directly affects temporal resource acquisition and plant growth (Chabot and Hicks, 1982; Kikuzawa and Ackerly, 1999), and consequently, carbon cycling in ecosystems (Chabot and Hicks, 1982). Based on our results, we propose that Cerrado woody species can also be classified according to their leaf longevity into two functional groups: 'species with long-lived leaves' (median leaf longevity >15 months), which maintain their foliage for extended periods, and 'species with short-lived leaves' (median leaf longevity <15 months), which rapidly replace their foliage in synchrony with seasonal rainfall. However, future studies on the vegetative phenology of savanna species investigate the time of leaf production and fall, and thus, the age and longevity of the leaves, across a broader range of species.

Woody species generally produce long-lived leaves in dystrophic soils (Chabot and Hicks, 1982; Westoby *et al*., 2002). This adaptation is interpreted as a nutrient conservation strategy; the longer the leaf remains on the plant, the more nutrients are retained within the leaf biomass, ultimately reducing the maintenance costs of the leaves (Kikuzawa, 1991; Aerts and van der Peijl, 1993). However, as observed in this study and other studies in the Cerrado (Nascimento *et al*., 1990; Paulilo and Felippe, 1992; Franco *et al*., 2005), many species exhibit mean leaf longevity equal to or less than 1 year. Controlling leaf longevity is also a strategy to regulate nutrient retranslocation. Before leaf abscission, the retranslocation of N and P is high in woody species from the Cerrado (Nardoto *et al*., 2006). In a review study, Kikuzawa (1995) concluded that leaf longevity is lower when the photosynthetic leaf rate is high or decreases rapidly over time or when the cost of leaf construction is low (e.g. nutrient-rich environments). In the Cerrado, lower leaf longevity can be determined by higher photosynthetic rates in deciduous and semi-deciduous species, as evidenced by some studies (Franco *et al*., 2005). Therefore, the low availability of nutrients in the soil, combined with the retranslocation of some of these nutrients from the leaves to the storage organs, suggests high costs for leaf production in these species.

Leaf age structure

The different leaf age structures observed among the studied species may directly affect photosynthetic activity throughout the year. In *Miconia albicans* and *Miconia fallax*, the continuous presence of mature leaves allows year-round carbon acquisition. Conversely, species such as *O. hexasperma*, *S. ferrugineus* and *Myrsine guianensis* exhibited periods dominated by late-stage or developing leaves, probably reducing overall photosynthetic capacity. For *Blepharocalyx salicifolius*, *Byrsonima verbascifolia* and *K. coriacea*, the abrupt decline in total leaf number and the prevalence of young and senescent leaves during the dry season can substantially limit or even suspend photosynthetic activity for extended periods. These patterns suggest a continuum of temporal strategies for carbon assimilation among the nine species studied. At one extreme, evergreen species maintain photosynthetic activity throughout the year (drought-tolerant), whereas semi-deciduous species reduce their photosynthetic activity (drought sensitivity). At the other extreme, deciduous species completely cease photosynthetic activity (avoiding drought) during intense water limitation. Phenological studies in Cerrado woody communities similarly report higher frequencies of species with complete leaflessness and fewer species retaining leaves year-round (Lenza and Klink, 2006; Pirani *et al*., 2009; Silvério and Lenza, 2010). Thus, phenological strategies of drought sensitivity (escape) or complete deciduousness (avoidance) appear to be more effective in coping with seasonal water deficits in this environment.

Effects of climate and soil water on leaf dynamics

Our study demonstrates that local climatic seasonality and soil water availability affect leaf production differently across phenological groups, with evergreen species exhibiting distinct responses from semi-deciduous and deciduous species. However, analysing the isolated effects of each variable, we found that climatic factors (e.g. precipitation and VPD) best explained the differences in leaf production between phenological groups. Water availability in the two deeper soil layers affected leaf abscission in divergent ways across the phenological groups. These findings indicate that while climate primarily influences leaf production patterns, soil moisture dynamics play a crucial role in modulating the timing and intensity of leaf abscission.

The significant reduction in soil water content between 2 and 3 m depth – particularly between 1 and 2 m – indicates that deciduous and semi-deciduous species reduce their reliance on these intermediate soil layers to sustain leaf production during the peak of the dry season (mainly between September and October). This pattern is consistent with global assessments showing that woody plants adjust their water-uptake depth according to temporal changes in soil moisture availability, shifting to deeper layers as shallow soils dry, and that differences in water-uptake depth between deciduous and evergreen species are relatively small compared to differences driven by hydroclimatic context and plant size, with large trees generally accessing deeper water sources while smaller individuals rely more on the upper soil layers (Bachofen *et al*., 2024). Within this framework, the temporary reduction in water use from 1 to 2 m by deciduous and semi-deciduous species probably reflects a strategy to minimize competitive overlap during the most limiting period of the year.

At the end of the dry season, higher evaporative demand combined with minimal rainfall can increase water loss and reduce the photosynthetic efficiency of older leaves. This decline is attributable to the limited capacity of senescent leaves, particularly under strongly seasonal climates such as the Cerrado, to regulate stomatal conductance effectively (Oliveira *et al.*, 2005). Therefore, the reduction in leaf number within the canopies of semi-deciduous and deciduous species during the dry period serves as a mechanism to prevent dehydration, minimizes water loss via transpiration and promotes rehydration of internal tissues, as previously discussed. With the onset of the rainy season, precipitation rapidly replenishes water in the upper soil layers. However, during this early phase, semi-deciduous and deciduous species seemed to absorb water from depths exceeding 1 m. In contrast, herbaceous and grassy species, with shallower root systems compared to shrubs and trees (Siebert *et al.*, 2024), probably utilize water from the initial rains. This indicates that, despite high temperatures, strong evaporative demand and scarce water availability up to 1 m deep, semi-deciduous and deciduous species can produce new leaf cohorts by accessing water from deeper soil layers.

CONCLUSIONS

Leaf dynamics studies provide a more detailed understanding of the vegetative behaviour of Cerrado woody species than traditional phenological studies. However, the distinction between phenological groups can vary depending on which specific aspect of leaf dynamics is considered (abscission, production, longevity or age structure). Thus, classifying species solely on the basis of vegetative behaviour may oversimplify the complexity of leaf phenology in Cerrado woody plants. Our findings show that atmospheric water conditions influence leaf production and abscission differently among phenological groups. In evergreen species, leaf abscission is only weakly affected by reductions in precipitation during the dry season, whereas in semi-deciduous and deciduous species, abscission intensified under greater water stress. In contrast, leaf production in evergreen species was dependent on rainfall-driven recharge of surface soil water, while semi-deciduous and deciduous species produced new leaves during the peak of the dry season by accessing deeper soil water. These contrasting responses indicate the differential effects of climate on species with distinct phenological behaviours and the ability of deciduous and semi-deciduous species to access deeper water. These differences have important implications for the functioning of Cerrado woody vegetation in the face of current climate change. Projected reductions in rainfall, a prolonged dry season, and more frequent and intense drought events (Hofmann *et al.*, 2021; Rodrigues *et al.*, 2022) could more immediately and severely affect evergreen species that depend on soil water recharge to produce new leaves. Although these findings emphasize that leaf longevity, rather than categorical leaf habit alone, provides a more informative and mechanistic axis for understanding how tropical savanna species respond to climatic seasonality and soil water limitation, we recommend that future studies include a broader range of species to better capture the spectrum of variation in leaf dynamics.

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SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Figure S1: Images showing branches and marked leaves (A– D) for the study of leaf demography of woody species in the IBGE Ecological Reserve in Central Brazil. (A) branch of *Miconia falax* with adult leaves (AL); (B) branch of *Myrsine guianensis* with adult (AL) and young leaves (YL); (C) branch of *Ouratea hexasperma* with young (YL), adult (AL) and senescing (SL) leaves; (D) branch of *Roupala montana* with mature leaves completely consumed by caterpillars of *Eustena opaca* (Notodontidae) and new young leaves produced in the same branch. Figure S2: Partial residual plots showing the effects of luminosity, soil water availability (2 m), maximum temperature, minimum temperature and vapour pressure deficit on leaf abscission. Points represent partial residuals by phenological group, and coloured lines show the smoothed relationships adjusted for other model predictors. Figure S3: Partial residual plots showing the effects of luminosity, soil water availability (2 m), maximum temperature, minimum temperature and vapour pressure deficit on leaf flushing. Points represent partial residuals by phenological group, and coloured lines show the smoothed relationships adjusted for other model predictors. Figure S4: Residuals versus fitted values for the most parsimonious models describing (a) leaf abscission and (b) leaf production. The point distributions indicate no strong deviations from homoscedasticity. Figure S5: Leaf dynamics of evergreen (MICALB, MICFAL, MYRGUI), semi-deciduous (ROUMON, OURHEX, STYFER) and deciduous (BLESAL, BYRVER, KIECOR) woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. The grey area in the plot represents the dry season (May to September). Figure S6: Relationship between leaf number and soil moisture for leaf abscission and leaf flushing of species within phenological groups of woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. Table S1: Mean angle ($\bar{a}$) ± angular standard deviation (s.d.) and mean date of occurrence for leaf production of woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. N = number of leaves; r = average vector concentration. First annual cycle (October

2001 to September 2003); second annual cycle (April 2002 to March 2003). MIC ALB = *Miconia albicans*; MIC FAL = *Miconia fallax*; MYR GUI = *Myrsine guianensis*; OUR HEX = *Ouratea hexasperma*; ROU MON = *Roupala montana*; STY FER = *Styrax ferrugineus*; BYR VER = *Byrsonima verbascifolia*; BLE SAL = *Blepharocalyx salicifolius*; KIE COR = *Kielmeyera coriacea*. Table S2: Maximum (MAX) and mean ($x \pm$ s.e.) longevity (in months) of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. N = number of leaves; EVE = evergreen; SEM = semi-deciduous; DEC = deciduous. Averages followed by the same letter indicate significant equality of leaf longevity by the non-parametric test of multiple comparisons ($\alpha = 0.05$). Table S3: Comparison of survival curves of species within phenological groups of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. The P-values indicate the significance level for chi-square analyses. Table S4: Summary of the best linear model to predict leaf abscission within phenological groups of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. Adjusted R^2: 0.41, $F_{(9 \text{ and } 119)}$: 15.43, P-value: <0.001. TMIN = minimum temperature, 1 m = soil moisture from surface to 1 m depth. Table S5: Summary of the best fit linear model relating leaf production to environmental predictors within phenological groups of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. Adjusted R^2: 0.48, $F_{(9 \text{ and } 116)}$: 14.06, P-value: <0.001. LUMIN = luminosity, TMAX = maximum temperature, TMIN = minimum temperature, VPD = vapour pressure deficit, 2 m = soil moisture between 1 and 2 m depth. Table S6: Model attributes for the best models (delta AICs < 2) relating climate and soil moisture to leaf abscission of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. GF = phenological groups, TMAX = maximum temperature, TMIN = minimum temperature, VPD = vapour pressure deficit, 1, 2 and 3 m = water availability at 1, 2 and 3 m, df = degrees of freedom. Table S7: Model attributes for the best models (delta AICs < 2) relating climate and soil moisture to leaf production of nine woody species in a savanna of the IBGE Ecological Reserve, Central Brazil. gf = phenological groups, LUMIN = luminosity, PRECIP = precipitation, TMAX = maximum temperature, TMIN = minimum temperature, VPD = vapour pressure deficit, 1, 2 and 3 m = water availability at 1, 2 and 3 m, df = degrees of freedom.

DATA AVAILABILITY

The data that support the findings of this study are available in the Supplementary Data and under request to the corresponding author.

AUTHOR CONTRIBUTIONS

E.L. and C.K. conceived the ideas. E.L., C.K. and M.B. planned and designed the research. E.L. collected data. L.M., L.G., M.C.S. and D.S. analysed the data. E.L., L.M., L.G., M.C.S. and D.S. wrote the manuscript. All authors contributed to the final revisions.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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