Rodriguésia 74: e00412022. 2023
http://rodriguesia.jbrj.gov.br
DOI: http://dx.doi.org/10.1590/2175-7860202374019

Original Paper

Reproductive and vegetative phenology of the micro endemic *Stachytarpheta cassiae* (Verbenaceae)

Gesline Ferreira Guimarães[1,5], *Michellia Pereira Soares*[1,6], *Renata Moreira dos Santos*[2,7], *Fabíola Mendes dos Santos*[3], *Lorena Ashworth*[4,8], *Daniel Negreiros*[2,9], *Ramiro Aguilar*[2,4,10] & *Geraldo Wilson Fernandes*[2,11,12]

Abstract

The flora of the Brazilian rupestrian grasslands represents a hotspot of species richness and endemisms. *Stachytarpheta cassiae* (Verbenaceae), is a micro endemic species, from which nothing is known. Here, we quantified the activity and intensity of vegetative and reproductive phenophases throughout 12 months and tested for their seasonality and their relationship with local climatic variables. Both vegetative and reproductive phenophases were continuous. No seasonality was observed in the vegetative phenophases and none of them was influenced by climatic variables. Only flower buds and mature fruits' intensities showed seasonality in February (rainy season) and July (dry season), respectively. Accordingly, increased temperature and humidity combined explained increased production of flower buds whereas decreased rainfall explained increased mature fruits. Higher intensity in flower buds may respond to similar climatic conditions as other species in the community. However, *S. cassiae* is much different as it continues producing flowers continuously. Higher intensity of mature fruits in the dry season is expected as their seeds are abiotically dispersed. Due to constant flower and leaf production, *S. cassia* may be a key species for the conservation of many vertebrate and invertebrate species and for maintaining the biogeochemical functioning of the impoverished soils of the rupestrian grasslands.

Key words: conservation, Espinhaço mountain range, lengthy flowering, phenological events.

Resumo

A flora dos campos rupestres brasileiros representa um hotspot de riqueza de espécies e endemismos. *Stachytarpheta cassiae* (Verbenaceae) é uma espécie micro endêmica, da qual nada se sabe sobre sua história natural. Aqui, quantificamos ao longo de 12 meses a atividade e intensidade das fenofases vegetativas e reprodutivas e testamos sua sazonalidade e sua relação com as variáveis climáticas locais. Tanto as fenofases vegetativas quanto as reprodutivas foram continuas. Não foi observada nenhuma sazonalidade nas fases vegetativas e nenhuma delas foi influenciada por variáveis climáticas. Somente os botões florais e a intensidade de frutos maduros mostraram sazonalidade significativa em fevereiro (estação chuvosa) e julho (estação seca), respectivamente. Assim, o aumento da temperatura e umidade combinados explicaram o aumento da produção de botões florais, enquanto a diminuição da precipitação explicou o aumento dos frutos maduros. A maior

See supplementary material at <https://doi.org/10.6084/m9.figshare.22310752.v1>

[1] Instituto Federal do Norte de Minas Gerais - campus Salinas, Lab. Ecologia e Sistemática Vegetal, Salinas, MG, Brazil.
[2] Universidade Federal de Minas Gerais, Inst. Ciências Biológicas, Depto. Genética, Ecologia e Evolução, Ecologia Evolutiva & Biodiversidade, Belo Horizonte, MG, Brazil.
[3] Universidade Federal de Lavras, Depto. Silvicultura e Genética Florestal, Lab. Sementes Florestais, Lavras, MG, Brazil. ORCID: <https://orcid.org/0000-0002-5267-9938>.
[4] Universidad Nacional de Córdoba - CONICET, Instituto Multidisciplinario de Biología Vegetal, Córdoba, Argentina.
[5] ORCID: <https://orcid.org/0009-0002-8879-5882>. [6] ORCID: <https://orcid.org/0000-0002-1167-4540>. [7] ORCID: <https://orcid.org/0000-0001-7022-7022>.
[8] ORCID: <https://orcid.org/0000-0002-5659-2477>. [9] ORCID: <https://orcid.org/0000-0002-4780-2284>. [10] ORCID: <https://orcid.org/0000-0003-4741-2611>.
[11] ORCID: <https://orcid.org/0000-0003-1559-6049>.
[12] Author for correspondence: gwilson@icb.ufmg.br

intensidade dos botões florais pode responder a condições climáticas semelhantes às de outras espécies na comunidade. No entanto, *S. cassiae* é muito diferente, pois produz flores continuamente. É esperada maior intensidade de frutos maduros na estação seca, já que suas sementes são dispersas por vetores abióticos. Devido à produção constante de flores e folhas, *S. cassia* pode ser uma espécie chave para a conservação de muitas espécies de vertebrados e invertebrados e para a manutenção do funcionamento biogeoquímico dos solos empobrecidos dos campos rupestres.
Palavras-chave: conservação, Serra do Espinhaço, floração prolongada, eventos fenológicos.

Introduction

Plant species that comprise the flora of rupestrian grasslands are under risk of extinction as a result of the increasing anthropogenic environmental disturbances. Although they represent more than 5% of the Brazilian flora (Fernandes 2016; Fernandes *et al.* 2018), species from the rupestrian grasslands may undergo extinction as a consequence of synergistic disturbances among land-use and climate changes and the lack of management policies from public environmental organisms (Fernandes *et al.* 2014, 2018, 2020). Another aspect that contributes to this worrying scenario is the lack of scientific knowledge about the natural history of many of these species (see Fernandes 2016). Endemic species are among the most threatened ones, in particular those with restricted distribution areas. Many endemic species from rupestrian grasslands have only a single known population such as *Collaea cipoensis* Fortunato (Fortunato 1995), *Baccharis concinna* G.M.Barroso (Marques *et al.* 2002) or *Coccoloba cereifera* Schwacke (Moreira *et al.* 2010).

In order to develop conservation and restoration strategies of threatened ecosystems, it is fundamental to understand the natural history of focal species, particularly about their phenology (*e.g.*, Belo *et al.* 2013; Fernandes 2016). In this regard, phenological studies represent important tools for understanding the factors that influence reproduction and survival of plant species (Maderia & Fernandes 1999; Morellato *et al.* 2010). However, phenological studies in certain environments such as the rupestrian grasslands remain particularly scant, especially in endemic or threatened species (see Madeira & Fernandes 1999; Dutra *et al.* 2009; Miola *et al.* 2010). One plant genus of great relevance in the landscape of rupestrian grasslands is *Stachytarpheta* (S. Atkins) (Verbenaceae), as it interacts with a large number of animal species. Species from *Stachytarpheta* genus are generally shrubby or herbaceous with small colorful and showy flowers from intense purple to pale pink (Atkins *et al.* 1996; Barbola *et al.* 2006). Some species are considered ornamental or medicinal, such as *S. jammaicensis* (L.) and *S. cayennensis* (Rich.) Vahl (Rodríguez & Castro 1996).

Phenological studies with species of *Stachytarpheta* genus are still scarce, despite their high frequency in the rupestrian grasslands landscape. There are some studies about the floral biology of *Stachytarpheta maximiliani* Scham. (Barbola *et al.* 2006), and most of the studies in the genus are about pollination, floral visitors and their behavior, such as in *S. cayennensis* (Rich.) (Fonseca *et al.* 2006) and *S. glabra* Cham. (Antonini *et al.* 2005; Jacobi & Antonini 2008). The only phenological studies in the genus were also conducted in these two latter species (Jacobi & Antonini 2008; Fonseca *et al.* 2006). The focus of this research is the microendemic species *Stachytarpheta cassiae* (S. Atkins) from northern Minas Gerais, from which nothing is known about its natural history and phenology.

Our objective was to evaluate the periodicity of the phenophases of *S. cassiae* throughout the year in the rupestrian grasslands of the State Park Serra Nova in Minas Gerais, Brazil. We propose to i) analyze qualitatively and quantitatively the reproductive and vegetative phenologies of *S. cassiae*; ii) and to assess the relationship of phenological events with climatic variables.

Materials and Methods

The study was conducted in the State Park Serra Nova (SPSN), in the north of Minas Gerais. The SPSN has 50.956,29 ha, (15°36'42''S, 42°44'30''W). According to the nearest Climatic Station, 83395 - Janaúba, the mean annual temperature was 25 °C and the mean annual rainfall in the region was 769 mm, over the 1992–2014 period. There are two distinctive periods, a rainy and warm period from October to April, and another one dry and slightly colder from May to September. July is the driest month with a mean rainfall of 0.22mm, while December is the rainiest month with 174 mm of mean rainfall (Fig. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22310752.v1>).

The SPSN shows a striking transition between cerrado and caatinga domains, intermingled with rocky outcrops from the Espinhaço Setentrional mountains. The vegetation is characterized by physiognomies of the rupestrian grasslands, cerrado, campo cerrado, seasonal semideciduous forests (gallery forests) and seasonal deciduous forests (dry forest), with a clear stratigraphy of the vegetation in relation to the cliffs of the sierras. In the higher areas, the vegetation is typical of the rupestrian grasslands. Litholic soils and cambisols predominant in the area (IEF 2003). Drummond *et al.* (2005) consider the SPSN as a valuable region for scientific research given the high richness of endemic and threatened plant species. Phenological data were obtained in two sites within the SPSN, one located in the lowlands, known as "Escorregador" (15°36'56.1''S, 42°44'00.8''W) at 818 m asl, with a population of 63 individuals of *S. cassiae* within an area of 0.06 ha. Another population was located in the higher lands of the SPSN at 1.059 m asl, known as "Miúdas" (15°36'24.9''S, 42°45'00.4''W), with 153 individuals in an area of 0.8 ha. Individuals from these two populations of *S. cassiae* were adults of 0.4–2.5 m height, with stem circumference at the bottom of 4–15 cm. Flowers show an intense blue color and are displayed in terminal spike inflorescences (Fig. 1). No other population of *S. cassiae* was found within the region.

Phenological events

Twenty adult individuals of at least 1.2 m height were marked from the two known populations: 10 from Escorregador and 10 from Miúdas. These individuals were located at a minimum distance of 10 m from each other in order to assure a higher genetic variability and less degree of consanguinity among them (Kageyama & Gandara 1999), prioritizing sexually mature individuals. All individuals had a fully visible crown and were georeferenced and marked with aluminum tags. From these 20 individuals, five were newly tagged and georeferenced during the seventh expedition, as the five originally marked individuals had died in April 2015 and needed to be replaced. From these new five individuals, two

Figure 1 – Adult individual of *Stachytarpheta cassiae* (Verbenaceae) in the rupestrian grassland, State Park Serra Nova, MG.

were from Escorregador and three from Miúdas population.

Phenological monitoring was conducted monthly, initiating in September 2014 until August 2015, completing 12 expeditions throughout one year. The vegetative phenology accounted for the events of foliar changes, starting with foliar budding, young leaves, adult leaves and senescence (Fig. 2). Foliar budding implies the start of the development of foliar buds, which is defined by an intense light-green coloration and slight purple line in the edge of new leaves. This period lasts until these leaves attain 0.40 cm (Fig. 2a). Young leaves, which appear from the end of foliar budding until reaching 1.5 cm length, present an obovate aspect, are showy light-green colored with an intense purple in the edges (Fig. 2b). Adult leaves are fully developed leaves with an oval foliar limb of up to 5 cm long, they have a dark green color with purple edges of little intensity (Fig. 2c). Senescent leaves are similar in size to adult leaves but with different color and withered appearance (Fig. 2d). These senescent leaves have a characteristic yellowish color and they do not have the purplish edges like the young and adult ones. Soon after or together with senescence, leaf fall occurs and many leaves fall under or around the canopy. These fallen leaves show an intense brown color, giving the impression of decay and death of the plant (Guitman *et al.* 1991).

The reproductive phenophases involved the flowering and fruiting processes, initiating with the formation of flower buds (Fig. 3a) and followed by flowers at anthesis (Fig. 3b). Flower buds are 1.23–1.98 cm long, have an intense purple color at the apex, extending from the lateral edges to the mid part of the flower bud. Flower buds are arranged in a terminal inflorescence with alternate organization within a spike. The flowers at anthesis are tubular, arranged in alternate shapes along the axis of the inflorescence and can reach up to 2.93 cm in length. Flowers have a purplish color and are very notorious at long distances, which is an important trait to attract pollinators. Flowers are 1.63–2.18 cm long with a diameter of 0.72–1.1 cm.

Figure 2 – a-d. Vegetative phenophases of *Stachytarpheta cassiae* (Verbenaceae) in an area of rupestrian grassland in State Park Serra Nova, MG – a. foliar budding; b. young leaves; c. adult leaves; d. senescent leaves.

The fruiting phenophase implies immature and mature fruits. Immature fruits are developing fruits with a size from 0.90 to 1.1 cm long, with a visible persistent stylet in the fruit (Fig. 3c). These immature fruits have a characteristic light green color in the base and a light brown color at the apex, with a few light-purple spots. Mature fruits are dry, brownish, of 0.77–1.03 cm long (Fig. 3d).

Analysis of phenological data

Phenological data were analyzed using activity and intensity indices. The activity index (percentage of individuals) is the simplest method, which verifies the presence or absence of a given phenophase in the individual. This method also estimates the synchronicity among the individuals of a population (*e.g.*, Morellato *et al.* 1990). The greater the number of individuals manifesting the same phenophase at the same time, the greater the synchrony of the population. A phenological event is considered asynchronic when < 20% of individuals express the same phenophase; little synchronic when 20–60% of individuals express the same phenophase and highly synchronic when > 60% of the individuals in the population express the same phenophase (Bencke & Morellato 2002).

The intensity index was calculated using the method proposed by Fournier (1974). Values were obtained in the field through a semi-quantitative interval scale of five categories (0 to 4) and a 25% interval between each category, allowing the estimation of the intensity percentage of each phenophase in each individual as follows: 0 = absence of phenophase; 1 = intensity of 1 to 25%; 2 = intensity of 26 to 50%; 3 = intensity of 51 to 75% and 4 = intensity of 76 and 100%. At the

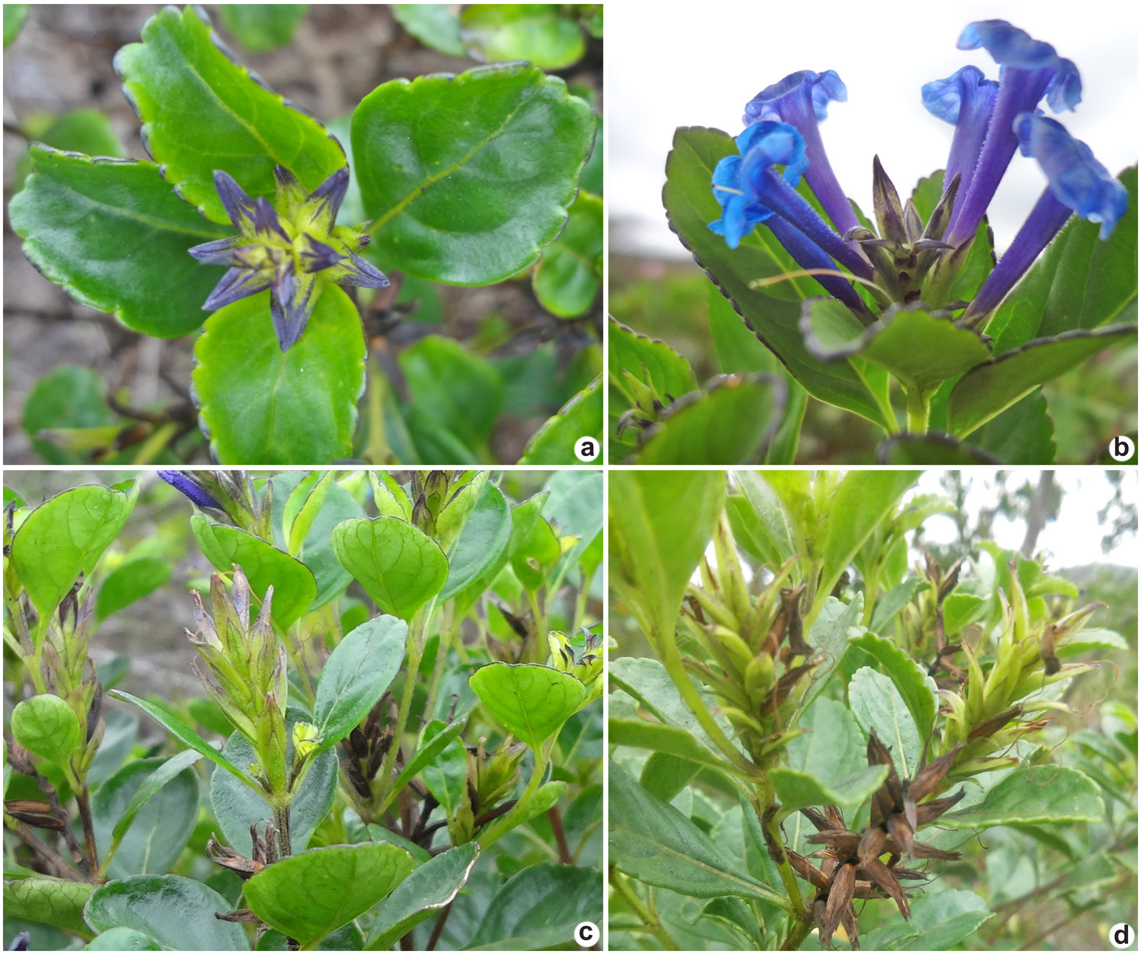

Figure 3 – a-d. Reproductive phenophases of *Stachytarpheta cassiae* (Verbenaceae) in an area of rupestrian grasslands in the State Park Serra Nova, MG – a. flower bud; b. flowers at anthesis; c. immature fruits; d. mature fruits.

end of each expedition, we summed the intensity values attributed to each individual, divided by the maximum intensity that can be reached by all individuals (N) in the sample (number of individuals multiplied by four). The value obtained, which corresponds to a proportion, was then multiplied by 100 to transform it into a percentage value, according to the formula: FI = (Σ grades) / (N*4) * 100.

Due to the cyclic nature of phenological data, we employed circular statistical analyses to calculate the existence of seasonality for each phenophase, following Morellato *et al.* (2010). The sampling months of each phenological event were converted into angles, where January corresponded to 0°, and December corresponded to 330°. We calculated the mean angle (and its corresponding month) of each phenophase, according to Morellato *et al.* (2010). The Rayleigh test (Zar 1996) was applied to test the significance of the mean vector angle (*i.e.*, mean date of each phenophase) with a unimodal distribution. When the mean vector angle is significant, it corresponds to the average date of the year around which the phenological events are concentrated and the pattern is interpreted as significantly seasonal (Morellato *et al.* 2010). The vector (r) varies from 0 to 1 and indicates the concentration of phenological events (*e.g.*, intensity) around the mean date or the degree of phenophases' seasonality (see Morellato *et al.* 2010). All circular analyses were done in the R environment (R Core Team 2022) using the "circular" package (Agostinelli & Lund 2017). The vegetative and reproductive phenologies of *S. cassiae* were classified according to Newstrom *et al.* (1994) as either continual, sub-annual or annual.

Finally, we assessed the influence of monthly mean temperature, humidity, rainfall and day length on the intensity of each reproductive and vegetative phenophase. Climatic variables were obtained from the Climatological Station 83395 - Janaúba, for the studied period (September 2014–August 2015; Fig. 4), with the exception of day lengths (hours), which were obtained from <http://www.solartopo.com/daylength.htm>, after providing the exact location of the study site and choosing the 15th day of each month. We used stepwise multiple regression analyses to determine the combination of climatic predictor variables that best predict the dependent (phenophase intensity) variables. Before running the analyses, we tested for multicollinearity among predictor variables and found that day length was positively correlated with temperature

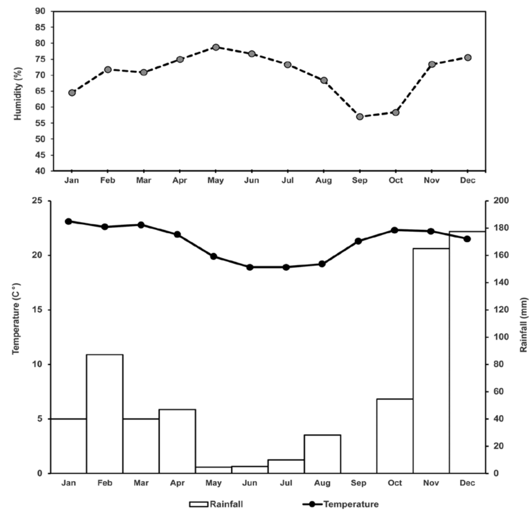

Figure 4 – Mean rainfall (mm) and mean temperature (ºC) for the studied period: September 2014–August 2015. Source: Climatic station 83395, Janaúba-MG.

(r = 0.85) and precipitation (r = 0.74; Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22310752.v1>). For that reason, we decided not to include day length in the models. The other three climatic variables were uncorrelated amongst them (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22310752.v1>). For each of the stepwise multiple regression analysis we tested for the assumptions of normality of residual errors and homogeneity of variances. Stepwise multiple regression models (forward, backward, both) were selected using the "stepAIC" function from the MASS package, which selects the best model by exact AIC. These analyses were conducted in R environment (R Core Team 2022).

Results

All *S. cassiae* individuals assessed presented the four vegetative phenophases, foliar budding, young leaves, adult leaves and senescent leaves, across the twelve months (Fig. 5a), which imply a high synchronicity among the individuals of each population. Similarly, these vegetative phenophases can be classified as continual at both the individual and population levels. Some of these phenophases appeared to show mild increases in their intensity in different months: foliar budding in February and October, young leaves in May and August, adult leaves in May, and senescent leaves in April and October (Fig. 5a). Nevertheless, according to the circular analyses, the four vegetative phenophases did not show any trace of seasonality. The Rayleigh tests on the four vegetative phenophases resulted in lengths of mean vector (r) lower than 0.1 with non-significant p-values (Tab. 1). The lower values of the length of mean vector (r) indicates an absence of temporal concentration of phenological activity. In other words, despite some apparent variation in intensities, the four vegetative phenophases in this species showed random or multi-modal pattern. Accordingly, the step-wise multiple regression models showed that none of the local climatic variables significantly explained variation in the intensity of any of the vegetative phenophases (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.22310752.v1>).

All individuals of *S. cassiae* also presented the four reproductive phenophases (flower buds, flowers at anthesis, immature fruits and mature fruits) across the twelve months of observation (Fig. 5b), implying a high synchronicity among the individuals of each population. These reproductive phenology patterns can also be classified as continual at both the individual and population levels. All of these reproductive phenophases showed visual variations in their intensity across the studied year: flower buds in May, flowers at anthesis in November, immature fruits in March, and mature fruits in July (Fig. 5b). Based on the circular analyses for the reproductive phenophases, we found a significant pattern of seasonality in the flower buds and mature fruits phenophases (Tab. 1). The mean vector angle corresponded to February for flower buds and to June for mature fruits (Tab. 1). On the other hand, the phenophases of flower at anthesis and immature fruits did not show any signs of seasonality (Tab. 1). Although the flower buds and mature fruits showed a significant seasonal pattern, the Rayleigh tests on the four reproductive phenophases resulted in lengths of mean vector (r) lower than 0.2 (Tab. 1), indicating a weak or absent temporal concentration of reproductive phenological activity in *S. cassiae*.

Step-wise multiple regression models showed that climatic variables significantly explained the reproductive phenophase intensities of flower buds ($R^2 = 0.644$; $p = 0.009$) and mature fruits ($R^2 = 0.759$; $p = 0.007$). None of the climatic variables influenced the intensity of flowers at anthesis and immature fruits across the year (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.22310752.v1>). The intensity of flower buds increased with both increasing temperature ($\beta = 2.98$; $t = 2.55$; $p = 0.031$) and humidity ($\beta = 1.01$; $t = 3.83$; $p = 0.004$). In contrast, the intensity of mature fruits decreased with increasing rainfall ($\beta = -1.13$; $t = -2.35$; $p = 0.044$).

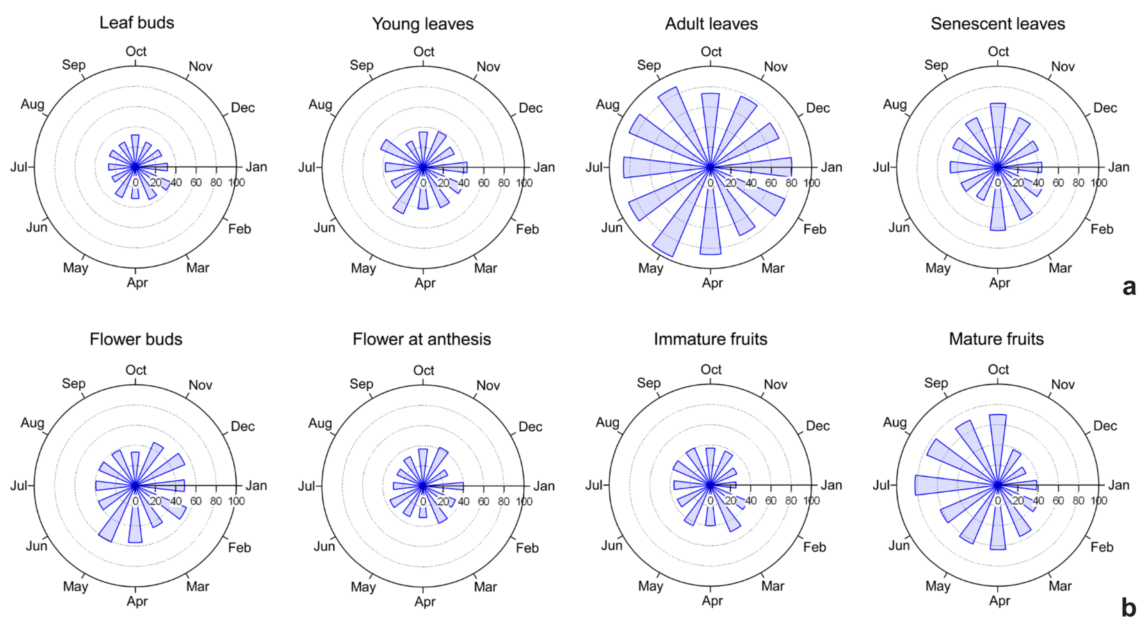

Figure 5 – a-b. Intensity index of phenophases in *Stachytarpheta cassiae* (Verbenaceae) in the rupestrian grasslands of the State Park Serra Nova, MG – a. vegetative; b. reproductive.

Table 1 – Results of the circular analysis to determine the seasonality of the phenophases of *Stachytarpheta cassiae* (Verbenaceae) in the rupestrian grassland, State Park Serra Nova, MG. Mean vector length (r) and significance (p-value) according to Rayleigh uniformity test ($\alpha = 0.05$). SD = standard deviation (degrees); NS = not significant.

Phenophase	Average date (month)	Mean vector angle	Circular SD	Mean vector length (r)	Rayleigh test (*p*)
Foliar buds	-	42.4°	131.8°	0.0708	NS
Young leaves	-	80.4°	135.0°	0.0623	NS
Adult leaves	-	151.0°	141.1°	0.0483	NS
Senescent leaves	-	301.9°	150.4°	0.0319	NS
Flower buds	Feb	52.0°	123.3°	0.0987	0.0048
Flower at anthesis	-	10.4°	141.1°	0.0483	NS
Immature fruits	-	125.0°	135.7°	0.0604	NS
Mature fruits	Jun	179.7°	107.5°	0.1721	< 0.0001

Discussion

All the vegetative phenophases of *Stachytarpheta cassiae* were present concomitantly throughout the year, indicating that leaf renewal is constant and highly synchronic among individuals. Plants with this characteristic are extremely important for the rupestrian grassland environment, as constant leaf renewal along with their senescence provides a source of organic matter for the poor and shallow soil of this ecosystem. Such potential increased nutritional input to the soil can offer a more suitable environment for the development of other species, in addition to decreasing soil temperature by increased shading.

None of the vegetative phenophases showed seasonality across the year and none of them was influenced by climatic variables. Seasonal vegetative phenological strategies seem to be more frequent in cerrado and seasonal forest realms, where woody plants usually increase leaf budding at the onset of the rainy season and peak leaf senescence during the dry season (Lenza & Klink 2006; Santos de Oliveira *et al.* 2021). The continuous vegetative phenophases of *S. cassiae* coincides with other woody species from the rupestrian grasslands (Santos de Oliveira *et al.* 2021). The capability of constant leaf production in such impoverished soils implies the development of morphological and ecophysiological strategies (*e.g.*, deep and efficient root system, the presence of reservoir organs such as xylopodia), that maximize the acquisition and maintenance of very limited resources (Belo *et al.* 2013; Dayrell *et al.* 2018). Thus, *S. cassiae* must have a greater tolerance to cope with water limitation, preventing increased leaf senescence during the dry season, which represents a nutrient conservation strategy in infertile environments, as observed in other species from the rupestrian grasslands (Dayrell *et al.* 2018; Santos de Oliveira *et al.* 2021). The constant production of leaves may also result in greater herbivory levels. However, growth defense tradeoff theory predicts that plants in low-resource habitats invest more energy in defense mechanisms against natural enemies than growth (Coley *et al.* 1985). Moreover, another defense strategy against herbivores involves the synchrony of leaf production at the population level (Aide 1993). This latter strategy can be effective if leaf biomass production exceeds the capacity of consumption by insects (Aide 1993; Lamarre *et al.* 2014). Thus, the high synchronicity of the vegetative phenophases along with other potential defense mechanisms may allow *S. cassiae* to cope with herbivory relatively well.

The production of flower buds showed a significant seasonality with a mean vector angle in February. Moreover, increased intensity of flower buds was explained by both increased temperature and humidity, which were highest between November and April, during the rainy period of warmer temperatures in the studied region. Such climatic conditions increase water availability, which along with constant leaf production would generate high resources to boost flower production (Batalha & Martins 2004; Belo *et al.* 2013). In fact, flowering onset and peak during the rainy season seem to be common for many species in the seasonal rupestrian grasslands and cerrado realms in Brazil, which are followed by a dry season of water shortage (Batalha & Mantovani 2000; Batalha & Martins 2004; Dutra *et al.* 2009; Santana & Machado 2010; Santos de Oliveira *et al.* 2021). However, the flowering pattern at the community level starts in the rainy season and lasts only until the beginning of the dry season (Dutra *et al.* 2009; Belo *et al.* 2013; Le Stradic *et al.* 2018; Santos de Oliveira *et al.* 2021). Thus, while the higher intensity in flower buds may respond to similar climatic conditions as many other species in the community, *S. cassiae* differs much from the rest as it continues producing flowers, including flowers at anthesis, with a relatively constant intensity throughout the year.

Species with continual flowering patterns such as *S. cassiae* are rather infrequent among angiosperms, which usually show annual seasonal flowering periods that last from a few days to few months at the most (*e.g.*, Newstrom *et al.* 1994; Kang & Jang 2004; Le Stradic *et al.* 2018). However, such extended flowering period is reported for other *Stachytarpheta* species such as *S. cayennensis* (Rich.) J. Vahl in the Cerrado (Arruda *et al.* 2009) and *S. glabra* in rupestrian grasslands in southeastern Minas Gerais (Jacobi & Antonini 2008). On the other hand, Machado & Oliveira (2015) observed that the flowering of *S. gesnerioides* Cham occurred only from January to March in cerrado domains of central Brazil. Interestingly, extended flowering throughout the year were recorded in other species from the rupestrian grasslands, belonging to different botanical families such as *Jatropha* sp. (Euphorbiaceae), *Prosopis rubriflora* (Fabaceae) (De Freitas *et al.* 2013) and *Hohenbergia ramageana* (Bromeliaceae) (Santana & Machado 2010). The occurrence of these long-flowering species represents key resources for pollinators and florivores throughout the year as they provide predictable resources over time (Loyola *et al.* 2007). Such extended flowering pattern increases the number of floral visitor and pollinator species seeking pollen and nectar, improving the reproductive success of these plant species (Antonini *et al.* 2005; Loyola *et al.* 2007). Finally, prolonged and synchronized flowering of plant individuals within and among populations in *S. cassiae* can increase the chances of cross-pollination, enhancing the genetic diversity of the progeny (Kameyama & Kudo 2009).

The intensity of immature fruits showed no seasonality and was not affected by any climatic variable. This pattern indicates that fruit production is mostly dependent on the success of effective pollination. The intensity of mature fruits, however, showed a significant seasonality with a mean vector angle in June, during the dry season. Accordingly, rainfall explained the intensity of mature fruits, increasing the intensity as rainfall decreased. Such phenological pattern may be explained by the seed dispersal strategy of the species, as *S. cassiae* has schizocarp fruits that abiotically disperse their seeds once the mature fruits dry up and release their seeds. Thus, the higher probability of seed dispersal success is under low rainfall conditions during the dry season (*e.g.*, Mantovani & Martins 1988; Oliveira & Moreira 1992). A similar phenological pattern of mature fruits was observed in *S. cayennensis* (Fonseca *et al.* 2006) and in other Cerrado species (Mantovani & Martins 1988). Almeida-Cortez (2004) explains that in areas with a seasonal climate, wind dispersal is more common during the dry season, as humidity makes it difficult to release the seeds.

Stachytarpheta cassiae presented all the reproductive and vegetative phenological phases during the studied 12 month-period. This micro-endemic species is of great relevance for maintaining the biogeochemical functioning of the impoverished soils of rupestrian grasslands as it provides continued input of organic matter and vegetation cover for the soil. Finally, the constant availability of resources for a wide range of floral visitors seeking for pollen and nectar, as well as for florivores and herbivores throughout the year, makes it a key species for the conservation of many vertebrate and invertebrate species in the rupestrian grasslands.

Acknowledgements

We are grateful to CNPq, FAPEMIG, Anglo American and Vale, for their support.

References

Agostinelli C & Lund U (2017) R package "circular": circular statistics (version 0.4-93). Available at <https://r-forge.r-project.org/projects/circular/>. Access on 13 June 2022.

Aide TM (1993) Patterns of leaf development and herbivory in a tropical understory community. Ecology 74: 455-466.

Almeida-Cortez JS (2004) Dispersão e banco de sementes. *In*: Ferreira AG & Borguetti F (eds.)

Germinação: do básico ao aplicado. Artmed, Porto Alegre. Pp. 225-235.

Antonini Y, Souza HG, Jacobi CM & Mury FB (2005) Diversidade e comportamento dos insetos visitantes florais de *Stachytarpheta glabra* Cham. (Verbenaceae), em uma área de campo ferruginoso, Ouro Preto, MG. Neotropical Entomology 34: 555-564.

Arruda R, Florencio C, Figueiredo R, Lima MIS & Salvador NNB (2009) Composição e fenologia de espécies herbáceas nativas em reflorestamento heterogêneo. Floresta 39: 525-533.

Atkins S, Alves RJV & Kolbeck J (1996) Plants in peril 23: *Stachytarpheta sellowiana*. Curtis's Botanical Magazine 13: 33-35.

Barbola IDF, Laroca S, Almeida MCD & Nascimento EAD (2006) Floral biology of *Stachytarpheta maximiliani* Scham. (Verbenaceae) and its floral visitors. Revista Brasileira de Entomologia 50: 498-504.

Batalha MA & Mantovani W (2000) Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. Revista Brasileira de Biologia 60: 129-145.

Batalha MA & Martins FR (2004) Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). Australian Journal of Botany 52: 149-161.

Belo RM, Negreiros D, Fernandes GW, Silveira FAO, Ranieri BD & Morellato PC (2013) Fenologia reprodutiva e vegetativa de arbustos endêmicos de campo rupestre na Serra do Cipó, Sudeste do Brasil. Rodriguésia 64: 817-828.

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

Coley PD, Bryant JP & Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230: 895-899.

Dayrell RLC, Arruda AJ, Pierce S, Negreiros D, Meyer PB, Lambers H & Silveira FAO (2018) Ontogenetic shifts in plant ecological strategies. Functional Ecology 32: 2730-2741.

De Freitas TG, Souza CS, Aoki C, Arakaki LMM, Stefanello TH, Sartori ÂLB & Sigrist MR (2013) Flora of Brazilian humid Chaco: composition and reproductive phenology. Check List 9: 973-979.

Drummond GM, Machado ABM & Martins CS (2005) Lista da fauna brasileira ameaçada de extinção: incluindo a lista das espécies quase ameaçadas e deficientes em dados. Fundação Biodiversitas, Belo Horizonte. 158p.

Dutra VF, Vieira MF, Garcia FCP & Lima HC (2009) Fenologia reprodutiva, síndromes de polinização e dispersão em espécies de Leguminosae dos campos rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil. Rodriguésia 60: 371-387.

Fernandes GW (2016) The shady future of the rupestrian grassland: major threats to conservation and challenges in the Anthropocene. Ecology and conservation of mountaintop grasslands in Brazil. Springer International Publishing, Switzerland. Pp. 545-561.

Fernandes GW, Arantes-Garcia L, Barbosa M, Barbosa NPU, Batista EKL, Beiroz W, Resende FM, Abrahão A, Almada ED, Alves E, Alves NJ, Angrisano P, Arista M, Arroyo J, Arruda AJ, Oliveira Bahia T, Braga L, Brito L, Callisto M, Caminha-Paiva D, Carvalho M, Conceição AA, Costa LN, Cruz A, Cunha-Blum J, Dagevos J, Dias BFS, Pinto VD, Dirzo R, Domingos DQ, Echternacht L, Fernandes S, Figueira JEC, Fiorini CF, Giulietti AM, Gomes A, Gomes VM, Gontijo B, Goulart F, Guerra TJ, Junqueira PA, Lima-Santos D, Marques J, Meira-Neto J, Miola DTB, Morellato LPC, Negreiros D, Neire E, Neves AC, Neves FS, Novais S, Oki Y, Oliveira E, Oliveira RS, Pivari MO, Pontes EJ, Ranieri BD, Pinheiro Ribas R, Scariot A, Schaefer CE, Sena L, Silva PG, Siqueira PR, Soares NC, Soares-Filho B, Solar R, Tabarelli M, Vasconcellos R, Vilela E & Silveira FAO (2020) Biodiversity and ecosystem services in the Campo Rupestre: a road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspectives in Ecology and Conservation 18: 213-222.

Fernandes GW, Barbosa NPU, Alberton B, Barbieri A, Dirzo R, Goulart F, Guerra TJ, Morellato LPC & Solar RRC (2018) The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation 27: 2587-2603.

Fernandes GW, Barbosa NPU, Negreiros D & Paglia AP (2014) Challenges for the conservation of vanishing megadiverse rupestrian grasslands. Natureza & Conservação 2: 162-165.

Fonseca NG, Kumagai AF, Mielke H & Olaf H (2006) Lepidópteros visitantes florais de *Stachytarpheta cayennensis* (Rich.) Vahl (Verbenaceae) em remanescente de Mata Atlântica, Minas Gerais, Brasil. Revista Brasileira de Entomologia 50: 399-405.

Fortunato RH (1995) A new species of *Collaea* (Leguminosae: Papilionoideae: Phaseoleae: Diodeinae) from Brazil. Kew Bulletin 50: 795-799

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

Guitman MR, Arnozis PA & Barneix AJ (1991) Effect of source-sink relations and nitrogen nutrition on senescence and N remobilization in the flag leaf of wheat. Physiologia Plantarum 82: 278-284.

IEF - Instituto Estadual de Florestas (2003) Decreto s/ nº de 21 de outubro de 2003; Parque Estadual de

Serra Nova. Available at <http://www.ief.mg.gov.br/component/content/article/213-parque-estadual-de-serra-nova>. Access on 11 March 2023.

Jacobi CM & Antonini Y (2008) Pollinators and defense of *Stachytarpheta glabra* (Verbenaceae) nectar resources by the hummingbird *Colibri serrirostris* (Trochilidae) on ironstone outcrops in south-east Brazil. Journal of Tropical Ecology 24: 301-308.

Kageyama PY & Gandara FB (1999) Restauração, conservação genética e produção de sementes. *In*: Simpósio mata ciliar: ciência e tecnologia, Lavras, Anais. UFLA/FAEPE/CEMIG, Lavras. Pp. 59-68.

Kameyama Y & Kudo G (2009) Flowering phenology influences seed production and outcrossing rate in populations of an alpine snowbed shrub, *Phyllodoce aleutica*: effects of pollinators and self-incompatibility. Annals of Botany 103: 1385-1394.

Kang H & Jang J (2004) Flowering patterns among angiosperm species in Korea: diversity and constraints. Journal of Plant Biology 47: 348-355.

Lamarre GPA, Mendoza I, Fine PVA & Baraloto C (2014) Leaf synchrony and insect herbivory among tropical tree habitat specialists. Plant Ecology 215: 209-220.

Le Stradic S, Buisson E, Fernandes GW & Morellato LPC (2018) Reproductive phenology of two co-occurring Neotropical mountain grasslands. Journal of Vegetation Science 29: 15-24.

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.

Loyola RD, Antonini Y, Jacobi CM & Martins RP (2007) Disponibilidad de recursos florales en campos metalíferos: riqueza de especies, frecuencia de visitación y comportamiento de abejas. Bioikos 21: 41-50.

Machado AO & Oliveira PE (2015) Diversidade beta de plantas que oferecem néctar como recurso floral aos beija-flores em cerrados do Brasil Central. Rodriguésia 66: 1-19.

Madeira JA & Fernandes GW (1999) Reproductive phenology of sympatric species of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil. Journal of Tropical Ecology 15: 463-479.

Mantovani W & MARTINS FR (1988) Variações fenológicas das espécies do cerrado da Reserva Biológica de Moji Guaçu, estado de São Paulo. Revista Brasileira de Botânica 11: 101-112.

Marques AR, Fernandes GW, Reis IA & Assunção RM (2002) Distribution of adult male and female *Baccharis concinna* (Asteraceae) in the rupestrian fields of Serra do Cipó, Brazil. Plant Biology 4: 94-103.

Miola DTB, Correia HVL, Fernandes GW & Negreiros D (2010) Efeito do fogo na fenologia de *Syagrus glaucescens* Glaz. *ex* Becc. (Arecaceae). Neotropical Biology and Conservation 5: 146-153.

Moreira RG, McCauley RA, Cortés-Palomec AC, Fernandes GW & Oyama K (2010) Spatial genetic structure of *Coccoloba cereifera* (Polygonaceae), a critically endangered microendemic species of Brazilian rupestrian fields. Conservation Genetics 11: 1247-1255.

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, Leitão Filho HF, Rodrigues RR & Joly CA (1990) Estratégias fenológicas de espécies arbóreas em floresta de altitude na Serra do Japi, Jundiaí, São Paulo. Revista Brasileira de Biologia 5: 149-162.

Newstrom LE, Frankie GW & Baker HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica 26: 141-159.

Oliveira PE & Moreira AG (1992) Anemocoria em espécies de cerrado e de mata de galeria. Revista Brasileira de Botânica 15: 163-174.

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.r-project.org/>. Access on 13 June 2022.

Rodríguez M & Castro O (1996) Pharmacological and chemical evaluation of *Stachytarpheta jamaicensis* (Verbenaceae). Revista de Biología Tropical 44: 353-359.

Santana CS & Machado CG (2010) Fenologia de floração e polinização de espécies ornitófilas de bromeliáceas em uma área de campo rupestre da Chapada Diamantina, BA, Brasil. Revista Brasileira de Botânica 33: 469-477.

Santos de Oliveira C, Messeder JVS, Teixido AL, Arantes MRR & Silveira FAO (2021) Vegetative and reproductive phenology in a tropical grassland-savanna-forest gradient. Journal of Vegetation Science 32: e12997.

Zar JH (1996) Bioestatistical analysis. Prentice-Hall, New Jersey. 662p.

Area Editor: Dr. André Rech
Received in April 07, 2022. Accepted in September 05, 2022.