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Original Article

Effects of an accidental dry-season fire on the reproductive phenology of two Neotropical savanna shrubs

P. Dodonov[a,b]*, *C. B. Zanelli*[c] *and D. M. Silva-Matos*[b]

[a]Laboratório de Ecologia Aplicada à Conservação, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, Km 16, Salobrinho, CEP 45662-900, Ilhéus, BA, Brazil

[b]Departamento de Hidrobiologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos, Rodovia Washington Luis, Km 235, Monjolinho, CP 676, CEP 13565-905, São Carlos, SP, Brazil

[c]Independent researcher

*e-mail: pdodonov@gmail.com

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(With 2 figures)

Abstract

Fire is a recurrent disturbance in savanna vegetation and savanna species are adapted to it. Even so, fire may affect various aspects of plant ecology, including phenology. We studied the effects of a spatially heterogeneous fire on the reproductive phenology of two dominant woody plant species, *Miconia albicans* (Melastomataceae) and *Schefflera vinosa* (Araliaceae), in a savanna area in South-eastern Brazil. The study site was partially burnt by a dry-season accidental fire in August 2006, and we monitored the phenolology of 30 burnt and 30 unburnt individuals of each species between September 2007 and September 2008. We used restricted randomizations to assess phenological differences between the burnt and unburnt individuals. Fire had negative effects on the phenology of *M. albicans*, with a smaller production of reproductive structures in general and of floral buds, total fruits, and ripe fruits in burnt plants. All unburnt but only 16% of the burnt *M. albicans* plants produced ripe fruits during the study. Fire effects on *S. vinosa* were smaller, but there was a greater production of floral buds and fruits (but not ripe fruits) by burnt plants; approximately 90% of the individuals *of S. vinosa* produced ripe fruits during the study, regardless of having been burnt or not. The differences between the two species may be related to *S. vinosa*'s faster growth and absence from the seed bank at the study site, whereas *M. albicans* grows more slowly and is dominant in the seed bank.

Keywords: Cerrado, flowering, fruiting, *Miconia albicans*, *Schefflera vinosa*, woody plants.

Efeitos de um incêndio acidental de estação seca sobre a fenologia reprodutiva de dois arbustos savânicos neotropicais

Resumo

O fogo é uma perturbação recorrente em vegetação savânica e as espécies do cerrado são adaptadas a ele. Mesmo assim, o fogo pode afetar aspectos da ecologia vegetal, incluindo a fenologia. Nós estudamos os efeitos de um incêndio espacialmente heterogêneo sobre a fenologia reprodutiva de duas espécies lenhosas dominantes, *Miconia albicans* (Melastomataceae) e *Schefflera vinosa* (Araliaceae), em uma área de cerrado no Sudeste do Brasil. A área de estudo foi parcialmente queimada por um incêndio acidental na estação seca (agosto) de 2006. Nós acompanhamos a fenologia reprodutiva de 30 indivíduos queimados e 30 não-queimados de cada espécie, de setembro de 2007 a setembro de 2008, usando aleatorizações restritas para comparar os dois grupos. Em *M. albicans*, a produção de estruturas reprodutivas como um todo e de botões florais, frutos e frutos maduros foi maior em indivíduos queimados do que nos não-queimados. Todos os indivíduos não-queimados, mas apenas 16% dos queimados, produziram frutos maduros durante o estudo. Já em *S. vinosa*, a produção de botões florais e de frutos (mas não de frutos maduros) foi maior em indivíduos queimados; aproximadamente 90% dos indivíduos de *S. vinosa* produziram frutos maduros durante o estudo, independentemente de terem sido queimados ou não. As diferenças entre as duas espécies podem estar relacionadas com o fato de *S. vinosa* crescer mais rápido e estar ausente do banco de sementes, ao contrário de *M. albicans*, de crescimento mais lento e dominante no banco de sementes.

Palavras-chave: Cerrado, floração, frutificação, *Miconia albicans*, Schefflera vinosa, plantas lenhosas.

1. Introduction

Fire is a recurrent disturbance in savannas worldwide (Dantas et al., 2016), and the plant species occurring in these environments have developed a number of adaptations to it (Hoffmann et al., 2003). However, although after-fire plant mortality in savanna vegetation such as the Brazilian *cerrado* tends to be low (Hoffmann and Solbrig, 2003), fires may decrease plant biomass (Hoffmann and Solbrig, 2003) and reproductive output (Hoffmann, 1998) as well as alter plant population dynamics (Hoffmann, 1999). Fires may be spatially heterogeneous, resulting in a mosaic of burnt and unburnt patches within an area (Wrobleski and Kauffman, 2003; Werner, 2010; Dodonov et al., 2014). Spatial variation in fire incidence may lead to spatial variation in plant characteristics such as plant allometry (Dodonov et al., 2011), size structure and distribution of resprouts (Silva et al., 2009; Dodonov et al., 2014), seedbank (Xavier, 2011), and plant phenology (Lucena et al., 2015).

Fire effects on plant phenology are of special importance, as phenology is a key determinant of the structure and diversity of mutualistic networks (Encinas-Viso et al., 2012). Therefore, a fire that alters the intensity and timing of flowering and fruiting will also affect the spatial and temporal distribution of resources available for different organisms. For example, a dry-season fire may destroy flowers and fruits and thus both prevent plant reproduction in the year it occurs and reduce the amount of resources available for nectarivorous and frugivorous animals. Depending on the species, this decrease in reproduction and resource availability may extend for several years after the fire (Hoffmann, 1998).

Fire effects on plant phenology and reproduction, however, may vary greatly among species. The reproduction of some species, especially in the grass and shrub layer, has been shown to be stimulated by fire in different biomes (Ward and Lamont, 2000; Lamont and Downes, 2011; Fidelis and Blanco, 2014). In the Brazilian *cerrado*, fire appears to stimulate flowering of the grass and subshrub layers (Munhoz and Felfili, 2005; 2007) but to inhibit the reproduction of woody plants (Hoffmann, 1998; Felfili et al., 1999). Fire effects may be expected to vary among species with different ecological and physiological characteristics, e.g. evergreen versus deciduous (Lucena et al., 2015), but it is also possible that they vary among similar plants growing in the same area (Hoffmann, 1998).

We assessed whether the reproductive phenology of two Neotropical savanna (Brazilian *cerrado*) shrub species, *Miconia albicans* (SW) Steud (Melastomataceae) and *Schefflera vinosa* (Cham & Schltdl.) Frodin & Fiaschi (Araliaceae), was affected by a dry-season fire that occurred one year before the beginning of study. We expected that, according to previous studies on *M. albicans* (Hoffmann, 1998; 1999), the time after the fire would not have been sufficient for the two species to recover, with smaller reproductive output by burnt plants. The two species are physiologically similar in a number of aspects: they are evergreen (Damascos et al., 2005; Lucena et al., 2015), respond to fire by intense resprouting which results in little difference in plant density between burnt and unburnt sites (Lucena 2009, Dodonov et al., 2014), produce small flowers (Goldenberg and Shepherd, 1998; Durigan et al., 2004), and produce small fleshy fruits which are likely to be dispersed mainly by birds (Durigan, et al. 2004; Allenspach and Dias, 2012). In addition, they are among the three most common woody plant species at the study site (Dodonov, 2015), indicating that they are highly adapted to the local environment. Therefore, differences in the phenological responses to fire of these two species may indicate different, but equally successful, ecological strategies.

2. Methods

2.1. Study site

We performed this study between September 2007 and September 2008 in a Brazilian *cerrado* fragment within the São Carlos *campus* of the Federal University of São Carlos, municipality of São Carlos, São Paulo State, Brazil (21°58'34"S, 47°52'31"W). The soil is acidic, with low nitrogen and high aluminium contents (Dantas and Batalha, 2011). The climate is subtropical with dry winters and wet summers, an annual rainfall of 1,339 mm and a mean annual temperature of 22.1° C (Oliveira and Batalha, 2005). The vegetation consists of typical *cerrado*, characterized by a discontinuous canopy layer up to 5 m high and a more or less continuous ground cover of herbaceous plants and subshrubs (Ribeiro and Walter, 2008). Part of the study site was occupied by an eucalypt plantation until approximately two decades prior to this study and is currently in an advanced stage of regeneration. On 26 August 2006, in late dry season, the study site was heterogeneously burned by an accidental fire which left a mosaic of burnt and unburnt patches of vegetation (Dodonov et al., 2014). Before the fire of 2006, the study site has been burnt at least once every four years (pers. comm. of University staff).

2.2. Study species

Miconia albicans (Melastomataceae) is a shrub or small tree with multiple stems that grows up to approximately 3.5 m tall at the study site (Dodonov et al., 2011). It is common in savanna and dry forest (*cerradão*) vegetation in Brazil (Oliveira and Batalha, 2005; Assunção and Felfili, 2004). It is an evergreen species (Damascos et al., 2005) that usually suffers nearly complete above-ground mortality in fires, which is followed by intense resprouting (Hoffmann and Solbrig, 2003; Dodonov et al., 2014). Fires also negatively impact seed production in the first year after a fire (Hoffmann, 1998). This species is apomictic, producing sterile pollen and receiving few visits by pollinators (Goldenberg and Shepherd, 1998). Its flowers are small and white and stay open for only a short period of time (Allenspach and Dias, 2012). It produces numerous small fruits which contain high levels of water and carbohydrates (Maruyama et al., 2007) and are consumed by at least 19 bird species (Allenspach and Dias, 2012). Its reproduction was observed to be inhibited in the first year after a fire but stimulated in the second and third years (Hoffmann, 1998).

Schefflera vinosa (Araliaceae) may be either a shrub or a tree (Durigan et al., 2004), with thin bark, that reaches a maximum height of 4 m at the study site (Dodonov et al., 2011). This species is also evergreen (Lucena et al., 2015) and occurs in different *cerrado* physiognomes (Soares et al., 2006). Its flowers are small, have a pale yellow color, are mostly odourless (Durigan et al., 2004), and are pollinated by numerous small insects (Martins and Batalha, 2006). It produces small, dark-brown fruits (Durigan et al., 2004). Its flowering and fruiting may be stimulated by fire (Lucena et al., 2015).

2.3. Data collection

We arbitrarily selected a total of 60 individuals of *M. albicans* and 60 individuals of *S. vinosa* in an approximately 70 x 200 m patchily burnt area at the study site (Dodonov et al. 2014). For this, we placed 6 transects on each side of a firebreak between a typical *cerrado* area and a *cerrado* area that regenerated after an eucalypt plantation. In each transect we selected up to five individuals, including both burnt and unburnt individuals when possible, with at least 5 m between adjacent individuals, to a total of 30 burnt and 30 unburnt individuals of each species. Burning was determined by noticing charcoal or signs of burning at the base of each individual. Most of the burnt individuals were probably resprouts, having been topkilled in the fire.

Approximately every two weeks (27 visits between 28 September 2007 and 22 September 2008), we recorded, for each individual, the presence or absence of reproductive structures in general (structures containing floral meristem, floral buds, flower and/or fruits), floral buds, flowers, total fruits, and ripe fruits. We also used five classes (0%, 1-25%, 26-50%, 51-75%, 76-100%; Fournier, 1974) to estimate the proportion of branches with reproductive structures; the proportion of reproductive structures with floral buds, flowers, and total fruits (green and ripe fruits combined); and the proportion of fruits that were ripe. We calculated the proportion of branches with floral buds, flowers, and fruits by multiplying the proportion of reproductive structures presenting these phenophases by the proportion of branches with reproductive structures, using the upper limit of each class. Further in the text, the values refer to the proportion of branches presenting each phenophase. Our method is thus an adaptation of Founier's method (Fournier, 1974), as, for each phenophase, we combined the proportion of branches with reproductive structures and the proportion of reproductive structures containing the phenophase in question.

2.4. Data analysis

We compared the phenology of burnt and unburnt plants for the proportion of branches presenting the following phenophases: fully developed inflorescences (excluding those that failed to develop and those composed only of floral meristem), floral buds, flowers, total fruits, and ripe fruits. For each sampling date, separately for burnt and unburnt plants, we calculated two indices: 1. the activity index, which is the proportion of individuals presenting a given phenophase; and 2. Fournier's intensity index (Fournier, 1974; Bencke and Morellato, 2002), calculated as the mean intensity of a given phenophase among the individuals. Both the activity index and the intensity index may assume values from 0 to 1. We calculated four summary statistics for the activity and intensity indices: mean value throughout the year; mean value without zeroes, considering only the time period when a given phenophase was present in at least one individual of the species and the group (burnt or unburnt); mean date of each phenophase, calculated as the mean angle after transforming the dates into radians; and temporal synchrony, calculated as the length of the mean vector of the transformed dates (Zar, 2010). High mean vector length values indicate low variation among individuals, i.e. high synchrony. We then compared these parameters between burnt and unburnt individuals by means of a randomization test (Manly, 2007) according to the following algorithm:

1) Calculate the activity and intensity indices for the burnt and unburnt plants for each date and calculate the corresponding summary statistics;
2) Calculate the observed difference between the burnt and unburnt plants for each of the summary statistics. We used circular range for the mean angles and simple differences for the other statistics;
3) Randomly classify each individual as either burnt or unburnt, keeping the total number of individuals within each group;
4) Repeat steps 1-3 on the randomized data sets a large number of times.

We used 4999 randomizations and calculated one-tailed significances from the distribution of the randomized values and the observed one, and calculated two-tailed significance (P) as two times the smallest of the one-tailed significances (Manly, 2007). For the difference between the mean angles, which is calculated in absolute values, we calculated significance as the proportion of all differences (the observed and the randomized ones) that were greater than or equal to the observed difference. Small significance values (e.g. $P \leq 0.05$) are interpreted as evidence for the difference between the two groups; the smaller the P value, the stronger the evidence (Manly, 2007).

We also used a randomization test to assess whether the activity and intensity indices were uniformly distributed throughout the year, for burnt and unburnt plants separately. For this, we compared the mean vector length of each phenophase with the distribution of vector lengths obtained by randomly reordering the indices. Vector lengths significantly larger than would be expected under the null hypothesis indicate a non-uniform distribution (Zar, 2010). As above, we used 4999 randomizations.

We performed these analyses with the software R 2.14.2 (R Core Team, 2015), using the package CircStats (Lund and Agostinelli, 2012) to calculate the circular statistics. The codes or the randomization analyses are available online at (Dodonov, 2017).

3. Results

For *M. albicans*, all unburnt individuals presented all phenophases except for flowers, which were not observed in 8 of the 30 individuals. Conversely, of the burnt individuals of this species, 10 did not produce ripe fruits, 10 did not produce either total or ripe fruits, 2 did not produce either flowers, total fruits or ripe fruits, and 3 did not produce any reproductive structures. For *S. vinosa*, all phenophases were observed in all unburnt individuals at some point except for ripe fruits, which were not observed in two individuals. For the burnt plants, three individuals did not produce ripe fruits and in one individual we did not observe flowers (but observed both green and ripe fruits), whereas reproductive structures in general and total fruits were observed in all individuals.

In *M. albicans*, unburnt individuals were more likely to produce reproductive structures in general, floral buds, total fruits, and ripe fruits (Figure 1), as shown

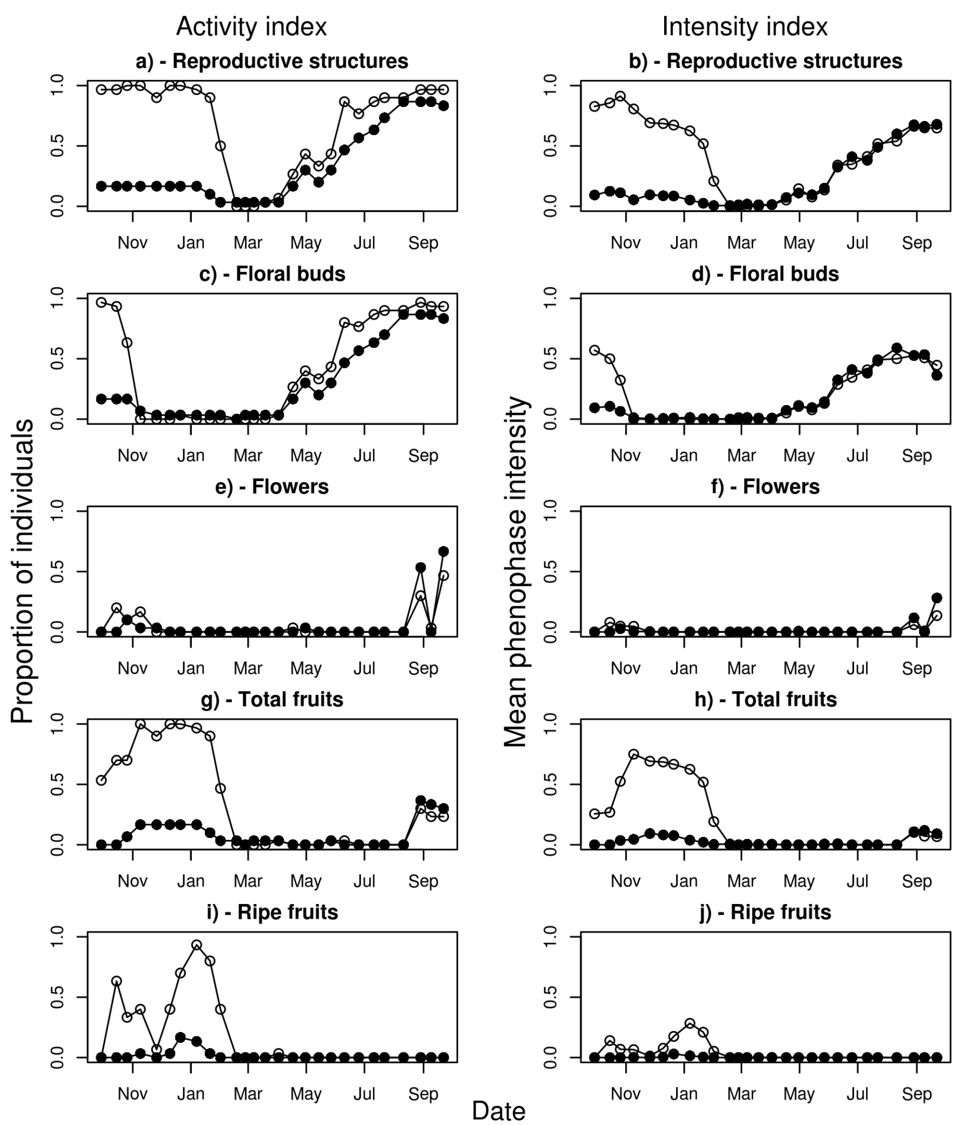

Figure 1. Reproductive phenology of unburnt (empty circles: ○) and burnt (filled circles: ●) individuals of *Miconia albicans* in a Neotropical savanna (Brazilian *cerrado*) area between September 2007 and September 2008, showing the proportion of individuals with each phenophase (activity index) and the mean intensity of each phenophase across all individuals (intensity index).

by the significant differences in the mean values of the activity indices for these phenophases between the burnt and unburnt plants (Table 1). The average intensity of reproductive structures in general, total fruits, and ripe fruits was also greater in the unburnt plants (Figure 1), with significant differences in the intensity indices (Table 1). Average flowering intensity was also greater in unburnt individuals (Table 1, Figure 1e). All phenophases, with the exception of ripe fruits, tended to be observed earlier in burnt plants (Table 1). The exception for ripe fruits was probably because the burnt individuals concentrated their fruit reproduction in 2008, whereas the unburnt individuals produced fruits both in 2007 and 2008 (Figure 1). Synchrony (as measured by the mean vector length) of reproductive structures in general and of ripe fruits was greater in burnt than in uburnt plants, with no significant differences observed for total fruits (Table 1). The intensity and activity indices of all phenophases deviated significantly from a random uniform distribution ($P < 0.03$), except for the intensity index of ripe fruits in burnt plants ($P = 0.06$) (Table 1).

Fewer differences between burnt and unburnt plants were observed for *S. vinosa* (Figure 2, Table 2). On average, there were more burnt *S. vinosa* individuals with floral buds and total fruits during its reproductive period and more unburnt individuals with flowers (Table 2). Conversely, the mean intensities of flowering (excluding zeroes) and of ripe fruit production (including zeroes) were slightly greater on unburnt individuals (Table 2). There were no significant differences in the mean date between burnt and unburnt plants except for the intensity index of ripe fruits, which peaked at an earlier date for the burnt plants (Table 2). Synchrony in the production of floral buds was greater in the unburnt plants (Table 2). The intensity and activity indices of all phenophases deviated significantly from a random uniform distribution ($P < 0.005$), except for the activity index of floral buds on burnt plants ($P = 0.10$).

Table 1. Summary statistics for the different phenophases of burnt and unburnt *Miconia albicans* individuals in a Neotropical savanna (Brazilian *cerrado*) area and the significance of the difference between the burnt and unburnt plants according to a randomization test. The activity index shows the proportion of individuals presenting a given phenophase and the intensity index shows the mean intensity of each phenophase among the individuals at a given time. The significance of the individual vector lengths are also shown, compared to a null model of random distribution of the phenophases throughout the year.

	Activity index			**Intensity index**		
	Unburnt	**Burnt**	**Significance**	**Unburnt**	**Burnt**	**Significance**
Reproductive structures in general						
Mean	0.67	0.31	0.0004	0.42	0.20	0.0004
Mean without zeroes	0.75	0.31	0.0004	0.47	0.20	0.0004
Mean date	Sep 25	Aug 04	0.0002	Oct 06	Aug 07	0.0002
Vector length	0.34***	0.54***	0.0004	0.50***	0.65***	0.0004
Floral buds						
Mean	0.41	0.28	0.0016	0.20	0.16	0.22
Mean without zeroes	0.65	0.29	0.0008	0.31	0.17	0.08
Mean date	Aug 05	Jul 29	0.10	Aug 14	Jul 27	0.0014
Vector length	0.63***	0.64***	0.95	0.71***	0.74***	0.49
Flowers						
Mean	0.05	0.05	0.81	0.01	0.02	0.58
Mean without zeroes	0.19	0.23	0.46	0.05	0.07	0.37
Mean date	Sep 20	Sep 08	0.017	Sep 24	Sep 10	0.004
Vector length	0.88**	0.90*	0.59	0.93***	0.97*	0.016
Total fruits						
Mean	0.33	0.08	0.0004	0.20	0.03	0.0004
Mean without zeroes	0.56	0.14	0.0004	0.34	0.05	0.0004
Mean date	Nov 17	Oct 17	0.0002	Nov 20	Oct 17	0.0002
Vector length	0.74***	0.56**	0.0004	0.81***	0.70**	0.0004
Ripe fruits						
Mean	0.17	0.01	0.0004	0.04	0.00	0.0004
Mean without zeroes	0.47	0.08	0.0004	0.11	0.01	0.0004
Mean date	Dec 06	Dec 14	0.15	Dec 09	Dec 15	0.30
Vector length	0.81***	0.96***	0.0004	0.83***	0.99^{ns}	0.0004

$^{ns}p > 0.05$. $^{*}0.05 \geq p > 0.01$. $^{**}0.01 \geq p > 0.001$. $^{***}p \leq 0.001$.

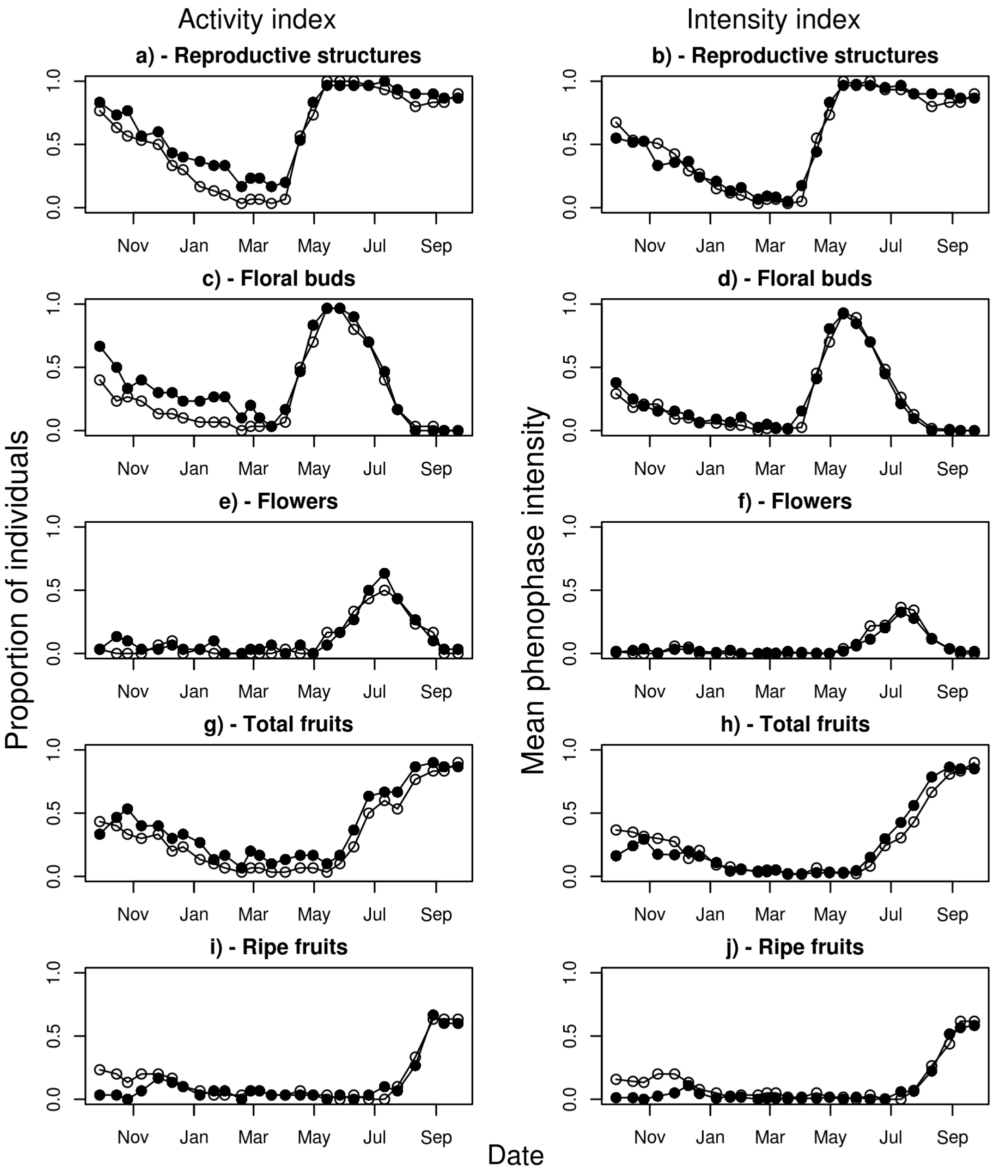

Figure 2. Reproductive phenology of unburnt (empty circles: ○) and burnt (filled circles: ●) individuals of *Schefflera vinosa* in a Neotropical savanna (Brazilian *cerrado*) area between September 2007 and September 2008, showing the proportion of individuals with each phenophase (activity index) and the mean intensity of each phenophase across all individuals (intensity index).

Table 2. Summary statistics for the different phenophases of burnt and unburnt *Schefflera vinosa* individuals in a Neotropical savanna (Brazilian *cerrado*) area and the significance of the difference between the burnt and unburnt plants according to a randomization test. The activity index shows the proportion of individuals presenting a given phenophase and the intensity index shows the mean intensity of each phenophase among the individuals at a given time.

	Activity index			Intensity index		
	Unburnt	**Burnt**	**Significance**	**Unburnt**	**Burnt**	**Significance**
Reproductive structures in general						
Mean	0.55	0.63	0.071	0.53	0.53	0.87
Mean without zeroes	0.55	0.63	0.060	0.53	0.53	0.88
Mean date	Jul 25	Jul 29	0.60	Jul 27	Jul 23	0.67
Vector length	0.39***	0.28***	0.078	0.41***	0.40***	0.88

nsp > 0.05. *0.05 ≥ p > 0.01. **0.01 ≥ p > 0.001. ***p ≤ 0.001.

Table 2. Continued...

	Activity index			Intensity index		
	Unburnt	Burnt	Significance	Unburnt	Burnt	Significance
Floral buds						
Mean	0.26	0.35	0.022	0.22	0.23	0.72
Mean without zeroes	0.30	0.42	0.001	0.25	0.27	0.58
Mean date	May 21	May 13	0.37	May 30	May 24	0.30
Vector length	0.50**	0.25^{ns}	0.045	0.54**	0.48**	0.58
Flowers						
Mean	0.10	0.12	0.22	0.06	0.05	0.59
Mean without zeroes	0.21	0.14	0.028	0.12	0.06	0.005
Mean date	Jul 02	Jul 08	0.42	Jul 05	Jul 09	0.56
Vector length	0.74***	0.60***	0.21	0.80***	0.75***	0.52
Total fruits						
Mean	0.30	0.39	0.076	0.25	0.25	0.91
Mean without zeroes	0.30	0.39	0.046	0.25	0.25	0.91
Mean date	Aug 29	Aug 28	0.93	Sep 06	Aug 27	0.15
Vector length	0.57***	0.42***	0.13	0.64***	0.64***	0.96
Ripe fruits						
Mean	0.15	0.12	0.27	0.13	0.09	0.051
Mean without zeroes	0.17	0.14	0.42	0.14	0.10	0.18
Mean date	Sep 17	Sep 09	0.35	Sep 19	Sep 03	0.042
Vector length	0.64***	0.60**	0.84	0.67***	0.83***	0.19

$^{ns}p > 0.05$. *$0.05 \geq p > 0.01$. **$0.01 \geq p > 0.001$. ***$p \leq 0.001$.

4. Discussion

Our results show that the reproductive phenology of *cerrado* woody plants may be affected by a previous fire event, but these effects are species-dependent. We demonstrated that although our two study species were ecologically similar in many aspects, the phenology of *M. albicans* was much more severly affected by the fire than that of *S. vinosa*: whereas the fire had overall negative effects on the phenology of *M. albicans*, its effects on *S. vinosa* could be null, positive, or negative depending on the phenophase being examined. All phenophases were non-uniformly distributed throughout the year in the burnt and unburnt individuals of both species; in the two cases when one of the indices (activity or intensity) complied with the random uniform distribution, the other did not.

Fire-stimulated flowering and reproduction have often been observed for subshrubs and herbaceous species in the *cerrado* (Munhoz and Felfili, 2005; 2007; Neves and Damasceno-Junior, 2011), but fire effects on woody plants vary from inhibition to stimulation of reproduction (Hoffmann, 1998; Felfili, et al. 1999; Franceschinelli and Bawa, 2005; Lucena et al., 2015). Our results corroborate this variation in the fire responses for woody species, which cannot be explained by factors such as growth form (Lamont and Downes, 2011), leaf deciduousness (Lucena et al., 2015), or seed dispersal syndromes (Lamont and Downes, 2011). However, some other ecological differences between our two species may aid in explaining the observed patterns.

Although both *M. albicans* and *S. vinosa* have the same general growth form and attain approximately the same maximum size (Durigan et al., 2004), they size may be differently affected by the fire. Thus, at the time of the study, burnt stems of *M. albicans* were in general smaller than burnt stems of *S. vinosa* at the study site (Dodonov et al., 2011), probably due to a slower resprout growth. The smaller resprout size of *M. albicans* may explain the smaller intensity of the reproductive phenophases of the burnt individuals as well as the failure of most of the burnt individuals to produce ripe fruits during the study period. In turn, *S. vinosa* is likely able to reattain reproductive size faster, with the burnt individuals reproducing more or less as succesfully as the unburnt ones.

Post-fire reproduction may also be related to the possibility of storing seeds in the soil seed bank (Lamont and Downes, 2011). In a four-year study of the soil seed bank at the study site, *M. albicans* was one of the two dominant species whereas *S. vinosa* was not detected (Xavier, 2011). *M. albicans* seeds were found in the soil seed bank of both burnt and unburnt patches, athough the fire apparently reduced their abundance (Dodonov et al., 2014). Thus, it is possible that, as *M. albicans* may colonize burnt patches from the seed bank, this species does not depend so heavily on the production of new seeds after a fire event. On the other hand, *S. vinosa* does not occur on the seed bank and new individuals can only originate from the production and dispersal of new seeds and fruits, leading to a necessity of more intense post-fire flowering and fruiting. In addition, as previously mentioned, both species are able to resprout after fire (Hoffmann and Solbrig, 2003; Lucena, 2009), indicating that they do not rely solely on sexual reproduction or soil seed banks for after-fire recovery.

In our study, the production of floral buds and of total fruits by *S. vinosa* was stimulated by the fire, whereas the production of flowers and ripe fruits was slightly inhibited. A different study in the same study site, however, observed more intense reproduction in the burnt individuals of this species (Lucena et al., 2015). Different explanations have been proposed for fire-stimulated flowering, including smoke, foliage loss, and an increase in the amount of resources in the soil (Lamont and Downes, 2011). Considering that the increase in reproduction was observed two years after the fire, the action of cues such as smoke and foliage loss is unlikely. We had a greater sampling size than Lucena et al. (2015) and our study was performed six months earlier, which may explain the differences between the two results. The combination of both studies indicates that a fire event does not have conspicuous effects, whether positive or negative, on the phenology of *S. vinosa* in a time span of two years. It is possible, for example, an increase in nutrient amount in the soil compensates for the fire impact.

Fire affected not only the number of individuals with a given phenophase at a time and the intensity of the different phenophases, but also the average date of the reproductive phenophases in *M. albicans* and, to a smaller extent, in *S. vinosa*. The burnt individuals of *M. albicans* reproduced mostly towards the end of the study, whereas the unburnt ones reproduced earlier in the study. The failure of most burnt individuals to produce ripe fruits corroborates this, as we interrupted our study before fruit ripening in 2008. Thus, at least two years may be needed for this species to recover from a fire event, similar to what was observed by Hoffmann (1998). This similarity occurred in spite of geographical differences between the two studies, as our study was performed in a more southern *cerrado* region.

In addition to affecting plant reproduction, fire may also putatively affect the pollinator and disperser communities of the study species. The small effect of fire on the flowering of *M. albicans* is probably due to its short flowering time as observed in this study, possibly related to this species' producing sterile pollen (Goldenberg and Shepherd, 1998). In turn, *S. vinosa* flowers are often visited by various insect species at the study site (pers. obs.), and the smaller activity and intensity indices of flowering in the burnt plants may putatively impact the pollinator community as well as decrease outcrossing (Franceschinelli and Bawa, 2005). Similarly, the lower fruit production by burnt individuals of *M. albicans*, especially considering that only five of the 30 burnt *M. albicans* plants produced ripe fruits during the study period, may have impacts on the frugivorous community, as the fruits of this species are consumed by at least 19 bird species at the study site (Allenspach and Dias, 2012).

In conclusion, we have observed that a spatially heterogeneous fire may result in spatial variation in the phenology of woody plants, and that these effects may vary between ecologically similar species. We propose that this variation in the fire effect between *S. vinosa* and *M. albicans* may be related to the differences in growth rate and presence in the soil seed bank between these two species (Xavier, 2011; Dodonov et al., 2011, 2014). Our results show that a dry-season canopy fire may result in spatial variation in the phenological patterns of some *cerrado* species but not others, creating a mosaic with flowering and non-flowering individuals which also depends on the species composition at the site.

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