



How does resprouting response differ among three species of savanna trees and in relation to plant size?

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Received: July 28, 2016

Accepted: December 5, 2016

ABSTRACT

Cerrado tree species can survive fire by resprouting. Generally, large and less damaged plants produce new branches and leaves from stem buds (aerial), whereas small and highly injured individuals would resprout from the stem base or from underground organs (basal). We compared the three most common Cerrado woody plant species in a savanna area of the IBGE Ecological Reserve, Brasília, Brazil, aiming to verify if the resprouting strategy (aerial or basal) differed between species and if that was related to plant size. *Guapira noxia* had small-sized plants, a higher percentage of trunk charred and more individuals with basal resprouting, while *Eriotheca pubescens* had large-sized plants with a greater intensity of aerial resprouting. Basal resprouting was associated with disturbance severity for *Dalbergia miscolobium*, while plant size was associated with aerial resprouting for *E. pubescens*. None of variables explained the variation in resprouting of *G. noxia*. The results showed that the post-fire regeneration strategy varied according to the species, confirming other studies of post-fire resprouting.

Keywords: Cerrado, disturbance, fire, resprout, size, tree

Introduction

Fire has been occurring in the Brazilian savannas (Cerrado) for 10 million years (Simon *et al.* 2009; Simon & Pennington 2012) and many Cerrado trees have survived fires because of traits such as thicker bark (Dantas & Pausas 2013) which protects stems from high fire temperatures and prevent topkill, or deciduous leaves that are less vulnerable to fire or herbivory damage (Lucena *et al.* 2015). Among Cerrado woody plants, the main consequences of burning are partial to complete loss of aerial biomass and, in more severe cases, plant death (Coutinho 1982; Hoffmann 1998; Hoffmann & Solbrig 2003; Hayashi & Appezzato-da-Glória 2007; Hoffmann *et al.* 2009). In this phytogeographic domain, tree species may survive fires by resprouting (from

basal, aerial and below-ground buds, Clarke *et al.* 2013) and resprouter species will have an advantage - compared to species growing from seeds - if burnings become more frequent (Ojeda *et al.* 2005).

Disturbance severity is perceived by a plant according to some characteristics, for instance the traits exemplified before, and also by plant size. The position of perennating buds is linked with bud protection (Raunkiaer 1934), and it may confer resilience to fire (Charles-Dominique *et al.* 2015) and facilitate escape from the fire-trap (repeated topkill and resprouting when fire is frequent: Grady & Hoffmann 2012). Instead small trees most strongly experience the impact of fire because their entire aboveground biomass is within the flame zone (Lawes *et al.* 2011). In contrast, large individuals are less affected by fire and may avoid topkill (Raw & Hay

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1985; Hoffmann 1998; Hoffmann & Solbrig 2003; Sato *et al.* 2010). Thereby large and less damaged plants would produce new branches and leaves from primary stem buds (aerial resprout following Clarke *et al.* 2013), whereas small and highly injured individuals of resprouting species would develop new trees from the stem base or from underground organs (basal resprout, Clarke *et al.* 2013). However, if burning is frequent, even some large mature individuals may be subjected to topkill and be unable to regrow rapidly before subsequent fire (Hoffmann & Solbrig 2003; Medeiros & Miranda 2005).

Disturbance severity is perceived by a community according to the species composition and their traits. These traits (physiological, regeneration and resistance traits) arranged in distinct ways represent different strategies of plants to survive fires (Cianciaruso *et al.* 2012). In this research, two strategies (basal and aerial resprout: Clarke *et al.* 2013) are studied and we expected to observe species-specific responses in post-fire resprouting, between three common woody plant species of the Cerrado, related to the plant size.

Several studies have evaluated the resprouting of Cerrado tree species after fire and they have showed that resprouting ability is species-dependent (Raw & Hay 1985; Salomão & Leite 1993; Hoffmann & Solbrig 2003; Medeiros & Miranda 2005; Hoffmann *et al.* 2009; Silva *et al.* 2009; Vale & Lopes 2010; Ribeiro *et al.* 2012). However, much of the existing research on regeneration following disturbances has focused on the role of other species rather than the woody species presented here (by the aforementioned authors), which are abundant species in most Cerrado physiognomies. Additionally, comparative studies relating post-fire responses to plant size are still scarce for these species. The incorporation of qualitative knowledge, such as the type of resprout (aerial or basal), could provide insights of the species ability to escape from the fire-trap and persist in areas experiencing higher frequency disturbances and inform post-fire management decisions. Thus, we aimed at verifying if the resprouting strategy (aerial or basal) differed between three woody Cerrado species and if that was related to plant size. We expected that large-sized individuals would resprout more from aerial buds, while small-sized ones would resprout basally and in higher frequency. Also, we aimed to observe if species changed the importance of strategies (basal and aerial resprouting) with time, as they recover after the disturbance.

Materials and methods

Site description

The study was performed at the IBGE (Instituto Brasileiro de Geografia e Estatística) Ecological Reserve, located 35 km south of Brasília, in the Federal District of Brazil

(15°55'-15°58'S and 47°52'-47°55'W), at an elevation of 1100 m. The Reserve encloses different Cerrado vegetation physiognomies, such as grasslands, savanna (cerrado *sensu stricto*), woodlands and gallery forests (Ribeiro 2011). The average annual rainfall recorded at IBGE meteorological station is 1461 mm (1980–2008), with a well-defined dry season from May to September and a mean annual temperature of 22.5 °C (Paiva *et al.* 2015). Soils at the reserve are deep well-drained oxisols.

Sampling design

The research was carried out at the boundary between gallery (i.e. riparian) forest and savanna. Six transects were positioned perpendicularly to the boundary; each transect was 10 m x 30 m and extended 30 m into the savanna. An accidental fire occurred in September 2011 and burned all individuals in savanna, which had only burned once in the previous 35 years due to a policy of fire suppression in the reserve.

The three most abundant species of the area were studied. *Dalbergia miscolobium* Benth. (Fabaceae) is a brevideciduous species distributed through the Brazilian savanna, which flowers in the end of the rainy season (March-April) and disperses its fruits at the end of dry season (Braz *et al.* 2009). *Eriotheca pubescens* (Mart. & Zucc.) Schott & Endl. (Malvaceae) is a deciduous, wind-dispersed, tree species, occurring in Cerrado areas of Central Brazil; it flowers from May to July and it fruits from October to November (Oliveira *et al.* 1992; Mendes-Rodrigues *et al.* 2005). *Guapira noxia* (Netto) Lundell (Nyctaginaceae) is a deciduous species, found in the cerrados and dry forests of Brazil, flowers from May to October and releases its fleshy fruits in November (Lorenzi 1992). In this study, 56 individuals were surveyed for *E. pubescens*, 30 for *D. miscolobium* and 16 for *G. noxia*. The sampling is not balanced in terms of species and it reflects the natural variation in population size showed by Fonseca & Silva Júnior (2004), comparing Cerrado sites in Jardim Botânico de Brasília, a contiguous area of cerrado to the IBGE Ecological Reserve. For each individual we measured charred height - the vertical extent of outer bark blackening - and size, represented by tree height and stem diameter. We also quantified the number of basal sprouts (BR) and we estimated the proportion of new leaves in the canopy, as an indication of aerial resprouting (AR). We estimated new leaves based on a percentage of the living canopy, using a semiquantitative index of phenophase intensity ranging from 0 (absence) to 4 (76-100 % of the canopy occupied by new leaves), with a 25% interval between each presence class (Fournier 1974). The first and second surveys were performed 13 February 2012, at the end of the wet season because plants had the entire growing season to resprout, and 31 November 2012, more than one year after burning, respectively. We assessed one commonly used indicator of fire severity and potential tree injury: the proportion of



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tree charred height (PCH: Catry *et al.* 2013).

Data analysis

Non-parametric tests were performed because our data did not fit a normal distribution. Wilcoxon signed-rank test was performed to compare parameters between species and years. Relationships between post-fire responses and explanatory parameters (Tab. 1) collected at the tree level were evaluated by calculation of Spearman's correlation coefficient. Statistical analyses were performed using the R version 3.2.1 (R-Development Core Team 2013).

Results

Mortality was low (two individuals in 102). *Guapira noxia* had small-sized plants, higher percentage of trunk charred and relatively more individuals with basal resprouts (38 % of the individuals resprouted from the base) than *D. miscolobium* and *E. pubescens* (Tab. 2). *Eriotheca* had large-sized plants, and consequently more leaves before burning.

BRs was lower in *G. noxia* and ARs was higher in *E. pubescens* (Tab. 2).

None of the independent variables explained the variation in the response parameters of *G. noxia* (Tab. 3). For *D. miscolobium*, PCH was positively correlated to BRs ($p=0.02$, Fig. 1A). For *E. pubescens*, diameter and height were negatively correlated to BRs ($p=0.02$ and $p=0.02$, respectively), while they were strongly positively correlated to ARs ($p<0.001$, for diameter - Fig. 1B, and height); leaf crop before fire was associated with ARs ($p=0.002$); and PCH was related to BRs ($p=0.001$) (Tab. 3).

Fourteen months after fire the number of basal resprouts (BRy) for the three studied species was not different from the five months post-fire (*D. miscolobium*: $p=0.50$; *E. pubescens*: $p=0.23$ and *G. noxia*: $p=0.13$). *E. pubescens* flushed vigorously after the first rains (ARs: about 75 % of the canopy with new leaves), but one year after this measurement we registered less leaves in the canopy (ARy: 50 % of the canopy had leaves, $p=0.01$); the other two species apparently did not produce or loose leaves in this period, as AR did not change with time (*D. miscolobium*: $p=0.25$ and *G. noxia*: $p=0.15$).

Table 1. Summary of the variables assessed for each tree.

Variable [code]	Units	Type
Tree regeneration status	4 cat. ^a	-
Number of basal resprouts at the end of the first growing season after fire (BRs)		R, E
Intensity of aerial resprouts at the end of the first growing season after fire (ARs)	5 cat. ^b	R, E
Number of basal resprouts one year after fire (BRy)		R
Intensity of aerial resprouts one year after fire (ARy)	5 cat. ^b	R
Leaves before fire	5 cat. ^b	E
Diameter at soil height	cm	E
Tree height	m	E
Percentage of charred height (PCH)	%	E

In Leaves before fire and AR: five categories: 0=0 %, 1=until 25 %, 2=until 50 %, 3=until 75 %, 4=until 100 % of the canopy occupied by leaves and branches. All data is given as median with first and third quartile. Values followed by the same letter do not differ amongst themselves following Wilcoxon signed-rank test.

Table 2. Plant Size, percentage of tree charred height (PCH), number of basal resprouts (BRs) and intensity of aerial resprouting in the growing season soon after fire (ARs) for each tree species.

Species	<i>D. miscolobium</i>	<i>E. pubescens</i>	<i>G. noxia</i>
Diameter (cm)	7 (7; 10) a	13 (11; 15) b	7 (6; 8) a
Height (m)	4 (4; 5) a	4 (4; 5) a	3(3; 4) b
PCH (%)	44 (32; 75) a	69 (40; 87) a	89 (62; 100) b
Leaves before fire	2 (1; 2) a	3 (3; 4) b	3 (1; 3) a
BRs	3 (1; 6) a	3 (1; 5) a	3 (1; 4) b
ARs	3 (0; 3) a	4 (3; 4) b	2 (0; 3) a

In Leaves before fire and AR: five categories: 0 = 0 %, 1 = until 25 %, 2 = until 50 %, 3 = until 75 %, 4 = until 100 % of the canopy occupied by leaves and branches. All data is given as median with first and third quartile. Values followed by the same letter do not differ amongst themselves following Wilcoxon signed-rank test.



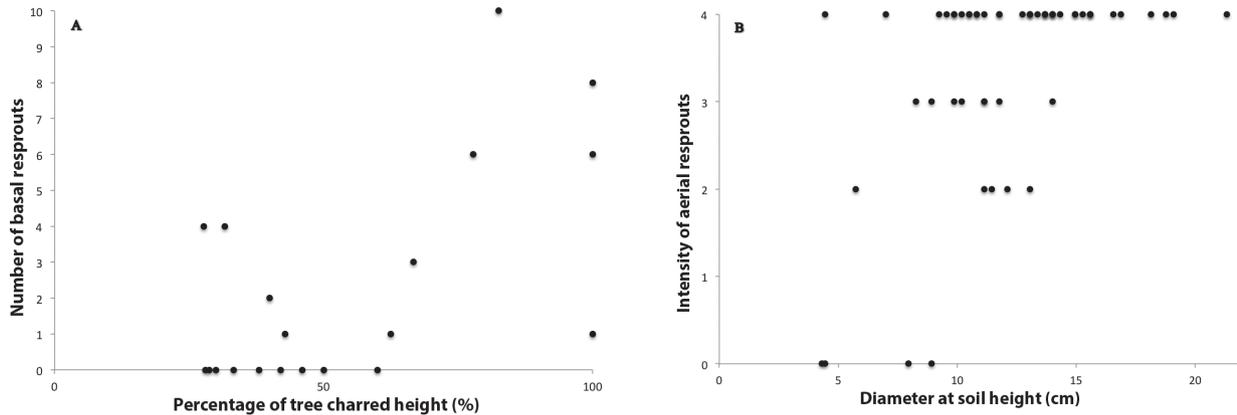


Figure 1. Relationships between the number of basal resprouts in the growing season soon after fire (BRs) and the percentage of tree charred height (PCH) for *Dalbergia miscolobium* (A) and between the intensity of aerial resprouting in the growing season soon after fire (ARs) and plant diameter for *Eriotheca pubescens* (B).

Table 3. Ro-values of the Spearman correlation between some variables for each tree species individually. Values in bold are significant.

	<i>D.miscolobium</i>		<i>E. pubescens</i>		<i>G. noxia</i>	
	BRs	ARs	BRs	ARs	BRs	ARs
Height	0.005	0.077	-0.302	0.560	-0.248	0.154
Diameter	-0.022	0.009	-0.315	0.547	-0.148	0.194
PCH	0.512	-0.407	0.421	-0.151	0.326	-0.399
Leaves before fire	-0.245	0.287	-0.190	0.404	-0.193	0.246

PCH=Percentage of tree charred height, BR=number of basal resprouts and AR=intensity of aerial resprouts, s: soon after fire.

Discussion

Our results confirm that stem mortality (topkill) of Brazilian savanna species is more prevalent than death of an individual (Hoffmann & Solbrig 2003). The vast majority of the studied individuals survived, persisting through resprouting, but we showed that the type (aerial or basal) and magnitude (in terms of numbers of resprouts) of the regeneration vary according to the species, plant size and damage severity.

Guapira noxia (that had 73 % of its plants smaller than 7.5 cm for stem diameter and shorter in height) suffered more severe damage and more individuals resprouted basally. Although for this particular species tree charred height and the number of basal resprouts were not related, the strategy of resprouting from stem base or underground tissues is a typical response to higher damage level and/or smaller plant size (Belingham & Sparrow 2000; Tredici 2001; Jancosky 2010; Vale & Lopes 2010; Ribeiro *et al.* 2012). *Dalbergia* and *Eriotheca* that had larger size individuals flushed and resprouted mainly from stem buds (personal observations), confirming other cerrado fire studies (Ribeiro *et al.* 2012).

These different regeneration strategies may have long-term structural and compositional consequences according

to variations in fire severity: under high-severity fires, the post-fire stature of Cerrado woody species would be reduced because of topkill and regeneration through basal resprouting; by contrast, low severity fires would cause less change due to aerial resprouting and high levels of survival. We believe Reserva Ecológica do IBGE experienced a medium severity fire because it has only burned once in the previous 35 years, the tree crowns were not scorched and consumed, but much of the dry phytomass concerning grasses and dry herbs were burnt (personal observations). Our results of aerial resprouting prevalent in *Eriotheca* and *Dalbergia* individuals and basal in *Guapira* ones can confirm the effects of this medium severity burning on abundant species of Cerrado and brought important insights about species-specific resprouting ability.

Guapira noxia had more individuals with basal resprout, but it also had lower resprout number per plant (one to four shoots). Other studies have shown an average of ten shoots for each *Tapirira guianensis* tree (Jancosky 2010) and some *Eucalyptus* species can produce up to 21 basal resprouts (Catry *et al.* 2013). For aerial resprouts some interesting differences appeared: individuals of *Guapira* and *Dalbergia* were not fully covered with new leaves and branches, and some had not flushed at all, after one entire post-burning growing season, surviving predominantly by basal resprouts, while *Eriotheca* intensively invested



in foliage after fire. This pattern may indicate that buds of *Eriotheca* species are more effectively protected from fire, confirming the findings of Charles-Dominique *et al.* (2015) that species with the most bud protection have greater canopy resprouting. Additionally, the greater the stem diameter: i) the more the number of apical buds (Lau 2009) of Cerrado woody species and consequently the higher the number of leaves (Farnsworth & Niklas 1995) and ii) relatively the higher the bark thickness providing stem insulation (Dantas & Pausas 2013). *Eriotheca pubescens* had 82 % of the individuals larger than 10 cm diameter, it may have had more apical buds and it had thicker bark (unpubl. res.) than the other two species.

Plant size (specifically diameter, height and, indirectly, leaf crop before fire) was related to the aerial resprouts only for *Eriotheca* (most of *Guapira* and *Dalbergia* plants were smaller than 7.5 cm, and probably younger individuals). The influence of size on post-fire plant flushing for this species corroborates many other Cerrado studies (Medeiros & Miranda 2005; Vale & Lopes 2010; Ribeiro *et al.* 2012). Although the relation was significant for only one species, pre-fire size may be a crucial factor determining how buds are protected during a burning event (Hoffmann & Solbrig 2003) - we again argue that *Eriotheca* buds seem more effectively protected than the other two species - and how much nutrients a plant can acquire from root storage tissues and relocate to aerial growth (Kennard *et al.* 2002). Regarding basal resprouts, the higher the fire damage severity of *Dalbergia* and *Eriotheca* trunks, the more resprouts the species produced (Bellingham & Sparrow 2000; Catry *et al.* 2013). Aerial and basal resprouts of *G. noxia* and *D. miscolobium* did not associate with any plant-size parameter, indicating that for these two species, and maybe for more Cerrado species, other factors not evaluated here can influence the resprouting strategy (like bark thickness: Pausas 2015).

One year after fire, the three studied species had the same number of basal resprouts than in the post-fire growing season. Other authors have shown that resprout senescence of Cerrado species may start within nine months, or as late as fourteen months (Cardinot 1988). Kauffman (1991) reported that plant resprouts of forest trees have died as the forest canopy restored. In fact, the shading of shoots by recovering vegetation and competition between resprouts can lead to senescence and mortality (Kauffman 1991; Vila & Terradas 1995), what we did not observe during the survey period.

The post-fire leaf crop of *Dalbergia* and *Guapira* did not change during the 13-month survey period. Typically fire incinerates or scorches old leaves, and plants produce new leaves just after the first rains (Vieira *et al.* 1996; Franco 1998). The three studied deciduous species (one is brevi-deciduous) commonly would have dropped their leaves in the dry season, but the high post-burning investment in canopy

reconstruction may have postponed this phenological event for next year's dry season. Also, water supply to leaves can be greater after fire, which could prevent leaf senescence (Schafer *et al.* 2014). Only *Eriotheca pubescens* had less leaves 14 months after fire. The anemochoric-fruit dispersal of this species, at the end of the dry season (October-November), is favored by leaf shedding (Oliveira & Moreira 1992) and less leaves in the canopy can be a strategy to maximize wind-dispersal.

Our results indicate that the resprouting patterns may vary in a burned community depending on the species. One could say that this species-specific response is actually a function of the species phenological state when the fire event takes place (Malanson & Trabaud 1988). *Dalbergia* was changing leaves, *Eriotheca* was fruiting and launching seeds and *Guapira* was flowering when fire burnt the study area. The reproductive phase is a resource-demanding plant life history stage and may impose harsh recovery constraints especially for *Eriotheca* and *Guapira*. In addition, other morphological attributes may be responsible for the different post-fire resprouting behaviour of the three studied species. The reconstruction of the large-sized and thick leaves of *Eriotheca* and *Guapira* compared to the small and smooth leaflets of *Dalbergia* represent other dissimilar strategies between Cerrado species that can represent extra costs for resprouting.

In summary, the post-fire regeneration strategy (aerial and basal resprouting) varied according to the plant size and damage severity between *Dalbergia*, *Eriotheca* and *Guapira* species, suggesting that other Cerrado woody species may also have distinct post-fire resprouting responses. Nevertheless, similar results relating the level of trunk fire injury and basal resprouting would probably be obtained for other species, as we found for two tree species in this study. It has been argued that Cerrado woody species occurring together and under similar environmental conditions would have close-related phenotypic traits (Silva & Batalha 2009). However, burning resistance strategies depend on historical fire regimes (especially fire frequency) that can lead to many different plant responses, as for example bud protection and bark thickness, not evaluated here and that still need to be better understood for Cerrado tree species. Knowing how trees respond to fire and what the factors are, such as the damage severity and plant size evaluated in this study, driving such responses is important for helping management decisions, particularly in Cerrado where fire is a recurrent disturbance.

Acknowledgements

We thank to CNPq (process number 140663/2012-6) and Capes (process number 17583/12-8) for funding, to the IBGE Ecological Reserve for permission to conduct research and to an anonymous reviewer for useful suggestions.



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