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The role of root buds in the regeneration of *Casearia sylvestris* Swartz (Salicaceae) in the Cerrado, São Carlos, São Paulo State, Brazil

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ABSTRACT - (The role of root buds in the regeneration of *Casearia sylvestris* Swartz (Salicaceae) in the Cerrado, São Carlos, São Paulo State, Brazil). The present work describes the fire effects on the population structure of *Casearia sylvestris* Swartz (Salicaceae). Diameter and height structure as well as spatial distribution patterns of the root sprouts were analyzed pre- and post-fire. The morphology and anatomy of the underground system were also analyzed in order to investigate the nature and origin of sprouts from this system. In this study, a 10-ha of Cerrado area was sampled from February to November 2006; in August, a fire burned roughly 80% of the study area, allowing us to compare the data collected pre- and post-fire. Our findings show that the underground systems consisted of specialized roots and buds originated close to the vascular cambium. The spatial distribution of the root sprouts became clustered pre- and post-fire and most of the root sprouts were concentrated in the first size class, indicating that the sprouts from roots play an important role in the recovery of this species in burnt areas.
Keywords: Cerrado, natural fires, sprouting, vegetative reproduction

RESUMO - (A função de raízes gemíferas na regeneração de *Casearia sylvestris* Swartz (Salicaceae) no Cerrado, São Carlos, SP, Brasil). Este artigo descreve os efeitos de incêndio na estrutura populacional de *Casearia sylvestris* Swartz (Salicaceae). Foram analisados a estrutura de diâmetro e altura e o padrão de distribuição espacial antes e após o fogo. Além disso, foi realizada a caracterização morfológica e anatômica do sistema subterrâneo para determinar a natureza e origem dos brotos oriundos desse sistema. Neste estudo foram amostrados 10 ha de fevereiro a novembro de 2006, em agosto, um incêndio queimou cerca de 80% da área de estudo, permitindo a comparação de dados coletados antes e após este evento. Foram verificados que os sistemas subterrâneos gemíferos são de natureza radicular e que os brotos se originam próximo ao câmbio vascular. A distribuição espacial dos brotos de raiz tornou-se agregada após o incêndio e houve maior concentração de brotos de raiz na primeira classe de tamanho indicando que esses brotos são responsáveis pela recomposição dessa espécie em áreas queimadas.
Palavras-chave: brotamento, Cerrado, incêndios naturais, reprodução vegetativa

Introduction

The Cerrado is the second most extensive phytogeographical domain in Brazil, occupying 21% of the land area, and it is considered the last agricultural frontier in the world (Borlaug 2002). Cerrado regions contain a mosaic of vegetation types, among which the savanna physiognomy prevails (67% of the total area), constituting the Cerrado *strictu sensu* (Coutinho 2006). The main abiotic determinants of the Cerrado are weathered, nutrient-poor acidic soils, markedly summer-wet periods and cooler temperatures, dry winters and recurring natural fires (Klink & Machado 2005, Haridasan 2008). Tree species in the Cerrado exhibit morphological and physiological adaptations to the periodic disturbances. Such adaptations include functionally herbaceous or woody geoxylic suffrutices with enlarged underground xylopodia or lignotubers, thick corky bark, pachycaul rosette-forming shrubs and trees with sparse branching, thick shoots and leaves concentrated at shoot tips, perennial herbs, and specialized flowering and fruiting phenologies (Simon *et al.* 2009). Plants subjected to water stress decrease their transpiration and thus their net photosynthesis (Prado *et al.* 2004).

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Cerrado fire events occur naturally during the wet season and are normally patchy, of low intensity and frequently self-extinguish rapidly (Miranda *et al.* 1993). On the other hand, when fire events occur on the dry season, often caused by human activity, the flames spread through a large amount of dry herbaceus layer, which fuels an intense fire (Miranda *et al.* 2002). The highest temperatures occur 60 cm above ground and range from 85 to 840 ºC (Miranda *et al.* 1993, 1996). Such fires damage shoots and leaves (mainly by the flow of hot air during the fire) or the whole individual plants. Soil temperature is around 50 °C, decreasing exponentially with depth and becoming negligible at and below a depth of 5 cm; therefore such insignificant soil temperature alterations are unlikely to have any direct effect on soil organic matter, microbial population, buried seeds (Mistry 1998) or the underground vegetative system.

The impact of fire affects a wide range of vital rates, including survival, growth, sexual reproduction and seedling establishment. Underground systems are protected in the soil, in a way that sprouting from an underground bud system, in the Cerrado post-fire, is a good ecological strategy (Hoffmann & Moreira 2002). According to Jeník (1994), vegetative reproduction of woody plants falls into three categories: the capacity of aerial branch reiteration (epicormic shoots), sprouting of basal portions of trunk (coppice shoots), and sprouting from root buds (root suckers or root sprouts). Root suckers (new stems originating from root buds at some distance from the main trunk) are much larger than seedlings and they should have a greater ability to survive throughout fire events (Hoffmann 1999). Thus, in the Cerrado, root buds may increase the population density by the production of root suckers which may lead to the recovery of burnt areas.

The occurrence of buds on the roots and the accumulation of energy reserves in such roots play a remarkably important role of adaptation for the survival of plants in the Cerrado (Rizzini 1997, Hayashi & Appezzato-da-Glória 2005). Root sprouting is associated with environmental disturbance and promotes structural changes in plant populations (Bellingham & Sparrow 2000, Hoffmann & Moreira 2002); it also alters the reproductive patterns of the clonal populations and decreases genetic diversity (Handel 1985), changing the balance between sexual and asexual reproduction (Hoffmann 1998).

A few studies have reported how fire affects the way in which woody species become established in the Cerrado. However, studies showed that fire events tend to increase the importance of vegetative reproduction in comparison to sexual reproduction (Hoffmann 1998, Silva *et al.* 2009). Palermo & Miranda (2012) observed that no flowers were produced by *Qualea parviflora* Mart. plants in the burned area, one year after a fire event, suggesting that this species may require more than a year to return to the normal reproductive cycle. As a matter of fact, the strategies of very few species have been investigated up to date; therefore additional studies regarding fire effects on the population structure of Cerrado species are quite essential to understand the behavior of such fire resistant species. In this study, the fire effects on the population structure of *Casearia sylvestris* Swartz (Salicaceae) were investigated. Our study was aimed at answering the following questions: *i*) What is the anatomical nature of the underground system from which sprouts arise? *ii*) Does the fire favor the production of shoots from such underground systems? *iii*) Does the fire change the diameter and height structure and spatial distribution pattern of *Casearia sylvestris*? To this end, the diameter and height structure and spatial distribution pattern were analyzed pre- and post-fire in the Cerrado. Furthermore, the morphology and anatomy of the underground system were characterized to investigate the nature and origin of sprouting.

Material and methods

Study area - Neotropical Cerrado in São Carlos, São Paulo State, Brazil (21º58'-22º00'S and 47º51'-47º52'W). Plant material was collected from the study area and the population structure of *Casearia sylvestris* was analyzed accordingly. The specimen exsiccate was deposited in the Herbarium of the Universidade Federal de São Carlos (HUFSCar) under accession number 8372. The local meteorological station recorded that the average annual rainfall and air temperature from 1992 to 2010 were 1,361.6 mm and 21.5 ºC, respectively. There are two well-defined seasons: a rainy season from October to March and a dry season from April to September (Monteiro & Prado 2006). Throughout the study period - from February to November 2006 - the total rainfall was 1,223 mm and the mean air temperature was 21 ºC. The topography of the area is gently rolling, at an average elevation of 850 m.a.s.l. The groundwater is at a depth of 10 m and the soil is classified as dystrophic latosol, nutrient-poor but rich in exchangeable aluminum (Kanno 1998). The vegetation is characterized by a woody layer formed by trees and bushes which protrude above a well-defined herbaceous layer (Ribeiro & Walter 1998).

Plant material - In the Cerrado, *Casearia sylvestris* Swartz. is a semi-deciduous tree reaching an average height of 164 cm (Souza *et al.* 2009). It occurs from Mexico to Argentina, with morphological variations in response to different habitats (Carvalho 2007). It is a common and widely distributed tree species in the Cerrado and forest areas (Ratter *et al.* 2003). Pharmacological importance is related to its antiulcer, anti-inflammatory, anti-snake venom and antitumor activity (Ferreira *et al.* 2011). Its wood is used as a fuel and is suitable to build fences, posts, stakes, rustic carpentry and tool handles (Torres & Yamamoto 1986).

Morpho-anatomy of the underground system - Root cuttings with sprouts of *Casearia sylvestris* were fixed in Randolph's CRAF (chromium-acetic-formalin), dehydrated in an ethanol series (Johansen 1940) and imbedded in paraffin. Transverse sections were cut from the blocks with a rotary microtome at a thickness of 10-12 µm. The sections were affixed with Bissing's adhesive (Bissing 1974). For permanent staining, the sections were deparaffinized in xylene and rehydrated in a decreasing ethanol series. Next, they were placed sequentially in 1% tannic acid, 3% iron chloride (Pizzolato 1977), 1% safranin and 2% astra blue (Gerlach 1969). The permanent sections were mounted with Apathy's syrup (sucrose and gum arabic) (Richards 1943). Histochemical tests were carried out by using macerated and fixed material or cross sections stained with Lugol's iodine, for the starch detection (Kraus & Arduin 1997). Photomicrographs of the material were taken with an Olympus PM-C35DX camera attached to an Olympus BX-41 optical microscope with micrometric scales being photographed and enlarged under the same optical conditions.

Population structure - Diameter and height structure and spatial distribution patterns of root sprouts of *Casearia sylvestris* were determined by the transect method. Two transects were systematically placed in 10 ha of the fire area in the Cerrado. These transects were 50 m long by 10 m wide, extending from a firebreak in a perpendicular position and 20 m apart. Plant individuals which sprouted from root buds and their sucker shoots were sampled along these transects. Sampling was done from February to November 2006. In August, an accidental fire burned roughly 80% of the study area, allowing data collected pre- and post-fire to be compared (sampling restarted in September). Such area had not been burned for approximately six years, during which much dry biomass had accumulated (Silva *et al.* 2009).

The underground systems were exposed with the aid of a hand-hoe in order to identify the main trunks and sprouts. Main trunks refer to plants growing from seeds, with an axial root (figure 1a), whereas the term root sprout or sucker designates an individual originating from a root bud (figure 1b). A tape measure and digital caliper were used to measure the total height above the soil and stem base diameter (SBD) of the root sprouts and main trunks as well as the distance between the two.

Mathematical and statistical data analysis - Population structure data for *Casearia sylvestris* were plotted on graphs based upon the distribution of height and stem base diameter. These variables were divided into size classes by using the equation: $A\ k^{-1}$, in which A is the difference between the largest and smallest values and k is the number of classes, defined by Sturges' formula $k = 1 + 3.3 \log_{10}n$, with n being the total number of individuals sampled.

Spatial distribution was analyzed by computing two indices: 1) Dispersion Index (DI), given by the formula $DI = S^2\ M^{-1}$, in which S^2 is the variance of the number of individuals, and M is the mean number of root sprouts); 2) Morisita Index (I_M), given by the formula $I_M = q \sum n(n-1).\ [N(N-1)]^{-1}$, with q being the total number of plots sampled, n being the number of individuals in the *i* plot and N being the total number of root sprouts sampled (N = 57 pre- and N = 34 post-fire). According to Brower & Zar (1984), DI can be influenced by the size of the population and plots, while I_M does not have this characteristic, not being affected by the random removal of population members. The spatial pattern is considered to be random when DI and $I_M = 1$; uniform if DI and $I_M < 1$ and clustered if DI and $I_M > 1$. Statistical significance of the differences between DI or I_M and one was tested by the chi-squared (χ^2) test, for non-normal data (Brower & Zar 1984). All the statistical tests were run in the statistical BioEstat 3.0 package (Sociedade Civil Mamirauá, CNPq).

Results and Discussion

The roots showed a secondary plant body, with a periderm, below which was the cortical parenchyma containing ducts, in direct contact with the secondary phloem. The secondary xylem showed solitary or multiple vessels and starch grains accumulated in the parenchymatic ray cells of the secondary vascular tissues as well as in the cortex. Furthermore, there was a primary xylem with centripetal maturation in the central region of *Casearia sylvestris* underground system, which corroborates that this organ was root-based (figure 2a).

Morpho-anatomical studies of the underground systems of plants from the Cerrado have shown the presence of gemmiferous underground systems, such as xylopodia and root buds (Hayashi & Appezzato-da-Gloria 2005, Vilhalva & Appezzato-da-Gloria 2006). Alonso & Machado (2007) described the morpho-anatomy and sprouting ability of the underground system of *Erythroxylum* species in the Cerrado. They found that sub-shrubby species occurred in clumps and had underground systems interlinked by soboles in *Erythroxylum nanum* and by xylopodia in *E. campestre*, while the shrubby species *E. tortuosum* grew isolated and highly branched with an underground system consisting of a primary root system near the soil surface. The authors concluded that the abundance of reserves and the bud-forming potential of the soboles, xylopodia and roots resulted in the production of vigorous branches, showing great value in the regeneration of the aerial biomass post-fire or seasonal drought in the Cerrado.

Above-ground biomass is eliminated post-fire, so that plants lose their photosynthetic capacity. In order to support respiratory demands and initiate sprouting, such plants shall have sufficient carbohydrates and nutrients stored in their underground organs (Bowen & Pate 1993). Moreira *et al*. (2012) while studying factors driving intraspecific variability in sprouting, found that resources stored by the plant pre-disturbance can boost its initial ability to sprout and the sprouting vigor and, consequently, its initial post-disturbance ability to acquire new resources. Likewise, the development of root buds depends on the resources stored by the main trunk. The present study showed that *C. sylvestris* root has starch grains which augment its ability to produce sprouts.

Casearia sylvestris root sprouts developed near the vascular cambium, which formed a ray of more dilated parenchyma internally (figure 2b). Hayashi & Appezzato-da-Glória (2009) observed various ways in which buds formed on planted root cuttings: close to the vascular cambium in *Centrolobium tomentosum*, from the callus in *Bauhinia forficata* and *Esenbeckia febrifuga* and by proliferation of the phloematic parenchyma in *Inga laurina*.

Based on the population under study, it was observed that vegetative reproduction prevailed over sexual reproduction in both pre- and post-fire (table 1). The spatial distribution of the *C. sylvestris* sprouts from roots pre-fire was in a random pattern, becoming clustered post-fire, according to both

Figure 1. a. Main trunk of *Casearia sylvestris* Swartz (Salicaceae) with primary root (arrow). b. sprouts (arrows) from root buds of *Casearia sylvestris*.

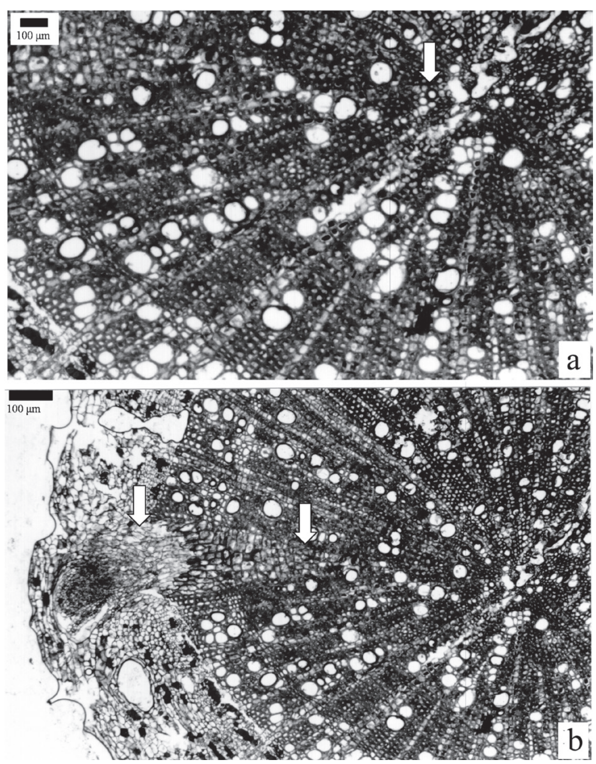

Figure 2. Microscopic image of transverse sections of root cuttings of *Casearia sylvestris* Swartz Swartz (Salicaceae). a. central region of the root with external metaxylem (arrows) and internal protoxylem (arrows). b. buds (arrows) forming in the root.

indices used (table 1). Sprouting from root buds could represent an effective strategy of spatial reoccupation and vegetative propagation; moreover, sprout shoots have the potential to emerge at variable distances from the main trunk and become independent plants (Rodrigues *et al.* 2004). Imatomi *et al.* (2009) reported that *C. sylvestris* seeds exhibit a low germination rate under laboratory conditions, whereas the presence of root buds may explain the wide distribution and high population density of this species. Furthermore, the potential of these buds for vegetative reproduction would enable the use of root cuttings to restore degraded areas. Hayashi & Appezzato-da-Glória (2009) demonstrated the ability of *Bauhinia forficata*, *Centrolobium tomentosum*, *Inga laurina* and *Esenbeckia febrifuga* roots to produce sprouts when they were cut into sections and isolated from the original plant.

Few studies of the spatial distribution of tree species in the Cerrado have found a clustered pattern (Hay *et al.* 2000, Souza & Coimbra 2005). The patterns of spatial distribution can be affected by biotic factors: vegetative propagation, seed dispersal, intra and interspecific interactions and varied development stages, and abiotic ones: light, temperature, soil, moisture, nutrients and environmental disturbances (such as fire, Melo *et al.* 2004). Hence, a particular pattern can result from one factor or the interaction of many (Grau & Veblen 2000). In our study, the spatial distribution pattern of *C. sylvestris* changed from random to clustered in response to the fire in the area. Some studies have shown that fire events damage plant aerial parts, causing a reduction in the amount of auxin reaching the roots, which in turn stimulates the development of sprouts (Bosela & Ewers 1997, Hoffmann & Moreira 2002, Rodrigues *et al.* 2004). The sprouts from the roots may then lead to a clustered pattern, since the mean distance between a main trunk and its sprouts depends on the energy cost of root production and the presence of spots favorable to their growth (Hutchings 1997).

The fire affected the diameter and height distribution of main trunks of *C. sylvestris* (figure 3 c, d, g and h). Prior to the fire, most individuals were concentrated in the intermediate classes of diameter and height (figure 3 c and d), while post-fire, the main trunks were concentrated in the larger size classes, indicating mortality of smaller individuals (figure 3 g and h). The diameter and height of *C. sylvestris* root sprouts were unaffected by the fire, and the largest concentration of sprouts pre- and post-fire were in the first size class (figure 3 a, b, e and f). The concentration of individuals in intermediate height classes, as found in the *C. sylvestris* main trunks, indicates reduction in recruitment and reproduction by seeds, although some individuals are reproductively mature and potentially able to maintain the stock of seeds in the area. According to Little & Wadsworth (1964), under good conditions *C. sylvestris* is capable of flowering and fruiting in the second year of life, when it reaches about 1 m height. Imatomi *et al.* (2009) observed that 77.8 % of *C. sylvestris* seeds were subjected to predation or aborted (unviable) and only 20% of the viable seeds sown in a greenhouse emerged. On the other hand, young root sprouts ensure the maintenance of the population, likely due to greater resistance to physical damage by root sprouts than by seedlings (Toivonen *et al*. 2011) and to rapid development, because their resources are drawn from the main trunk which is already established.

Environmental disturbances interfere in the reproductive strategy of plants by reducing the rate of reproduction by seeds and stimulating the formation and development of root buds (Kauffman 1991). Root sprouts grow rapidly as they are partly nourished by the root system of the main trunks. Seedlings require more time to become established since they are more exposed to adverse conditions (Kauffman 1991).

Table 1. Parameters of population structure of *Casearia sylvestris* Swartz (Salicaceae) plants in a Cerrado area (São Carlos, São Paulo State, Brazil) pre- and post-fire event.

	Before fire	After fire
Percentage of individuals with sprouts (%)	20	80
Number of sprouts per individual	3.6	10.2
Percentage of root sprouts (%)	78.26	91.1
Distance between sprouts and tree (cm)	11-172	29-177
Morisita index (I_M)	0.31	5.39
Dispersion index (DI)	0.86	1.94

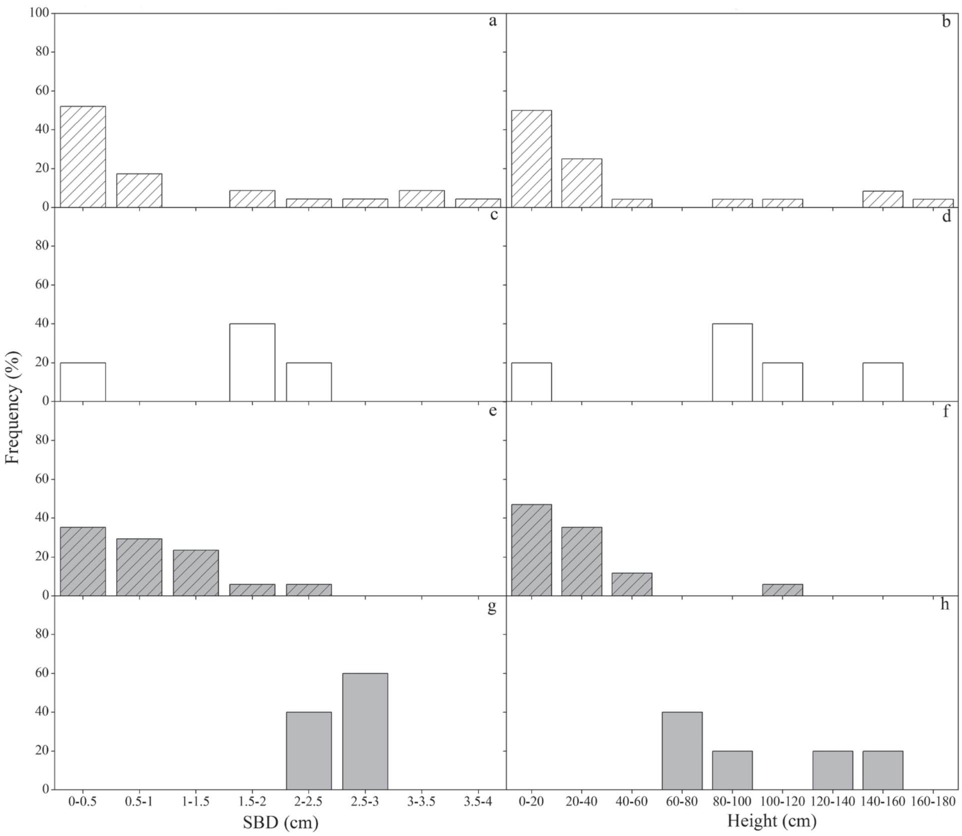

Figure 3. Distribution of stem base diameter (SBD) and height classes of *Casearia sylvestris* Swartz (Salicaceae) root sprouts and main trunks in a Cerrado area of the Universidade Federal de São Carlos (São Carlos, São Paulo State, Brazil), before and approximately one month after a fire event. Root sucker, Main trunk, Root sucker after fire, Main trunk after fire.

Therefore, environmental disturbances, particularly fire, can promote the growth of these root sprouts, offsetting the negative effect of the mortality of seedlings (Hoffmann 1999). Based on the population under study, the prevailing reproductive strategy was vegetative, 85% of the plants analyzed arising from root buds. Sprouting from roots is an important natural mechanism for regeneration just after a natural disturbance, because it quickly provides new plant cover in affected areas (Paciorek *et al.* 2000, Kennard *et al.* 2002).

Cerrado species have become adapted to fire events during evolution. Some plant species need fire events to flower, germinate or disperse seeds. Most Cerrado woody species, shoots and trunks show suberization, promoting insulation of internal tissues (Gottsberger & Silberbauer-Gottsberger 2006). An increase in vegetative reproduction (from root sprouts) with increasing fire frequency is one of several interactive adaptations of Cerrado woody species in response to disturbance. The present study has shown that the underground systems of *C. sylvestris* have the characteristics of root and sprouts originated close to the vascular cambium. The spatial distribution of the root sprouts became clustered post-fire and root sprouts were concentrated in the first size class, indicating that these sprouts play a major role in the recovery of this species in burned areas. Therefore, fire events favor the production of shoots from the underground systems. Furthermore, root sprouts are an important morpho-anatomical adaptation in the Cerrado, as they allow prompt colonization of burnt areas.

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