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# Resprouting of native species from Cerrado: a structural perspective

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Thesis presented to obtain the degree of Doctor in Science.
Area: Plant Physiology and Biochemistry

**Piracicaba**
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**Bachelor of Biological Sciences**

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# RESUMO

## Rebrotamento de espécies nativas do Cerrado: uma perspectiva estrutural

O rebrotamento é considerado o atributo regeneração mais importante para a persistência da vegetação em resposta a distúrbios ambientais, os quais são considerados comuns no Cerrado. Este atributo depende do desenvolvimento, grau de proteção das gemas e da mobilização de compostos de reserva presentes nos sistemas subterrâneos. Atualmente uma das ameaças mais importantes à vegetação do Cerrado é o cultivo de espécies exóticas comerciais, a exemplo do *Pinus* sp., o qual tende a reduzir drasticamente a ocorrência e desenvolvimento de espécies nativas pela sua alta capacidade competitiva. Essa situação vem ocorrendo na Estação Ecológica de Santa Bárbara (EEcSB), Águas de Santa Bárbara – São Paulo, que possui áreas de cultivo de *Pinus* sp. desde a década de 1970. Devido ao impacto negativo do *Pinus* sp. na vegetação do Cerrado, o plano de manejo do EEcSB (2011) vem trabalhando para eliminar gradativamente as espécies exóticas visando à regeneração da vegetação nativa. A partir dessa ação, espécies nativas como as palmeiras *Allagoptera campestris* (Mart.) Kuntze e *Syagrus loefgrenii* Glassman estão rebrotando principalmente nas áreas onde o material remanescente foi queimado após o corte raso das árvores. Além disso, é possível observar a presença dessas palmeiras coexistindo no sub-bosque de *Pinus* sp. No entanto, existem lacunas sobre as características que conferem resiliência e promovem a regeneração destas plantas. Desta forma, o presente estudo objetivou responder as seguintes questões: a) Quais são as características estruturais que permitiram a rebrota de espécies de Myrtaceae após anos de supressão dos órgãos aéreos pela presença das dos pinheiros? b) Após a rebrota, como os tecidos meristemáticos são protegidos nas gemas aéreas (terminais, axilares e acessórias) num ambiente em regeneração? c) Quais são as adaptações das espécies de palmeiras que as permitem colonizar e crescer em áreas com diferentes históricos de perturbação? d) As palmeiras são capazes de rebrotar nas áreas perturbadas após a introdução de uma nova perturbação?

Palavras-chave: Banco de gemas, Estratégias de regeneração, Myrtaceae, Gemas aéreas, Gemas acessórias, Proteção das gemas, Propagação vegetativa, Palmeiras geoxilas

# ABSTRACT

## Resprouting of native species from Cerrado: a structural perspective

Resprouting is considered the most important regenerative trait for vegetation persistency as a response to environmental disturbances, which are considered common in Cerrado. This functional trait depends on the development, the protection degree of buds, and also the mobilization of storage compounds presents in the belowground systems. Nowadays, one of the most severe threats to Cerrado vegetation is the cultivation of commercial exotic species, such as *Pinus* sp., which drastically reduce the occurrence and development of native species due to their highly competitive capacity. This situation has been occurring at the Santa Bárbara Ecological Station (EEcSB), Águas de Santa Bárbara - São Paulo, where there are *Pinus* sp. plantations since the 1970s. Due to the negative impact of *Pinus* sp. on the Cerrado vegetation, the EEcSB management plan (2011) has been working to gradually eliminate the exotic species with the purpose of regenerate the native species. Since this action, native species such as the palms *Allagoptera campestris* (Mart.) Kuntze and *Syagrus loefgrenii* Glassman have been resprouting mainly in those areas where the remaining material was burned after the clear-cutting of the trees. In addition, it is possible to observe the presence of these palms coexisting in the understory of *Pinus* sp. However, there are gaps in the features that confer resilience and promote the regeneration of these plants. Thus, the present study aimed to answer the following questions: a) Which are the structural features that allowed the resprouting of Myrtaceae species after years of the aerial organs being suppressed by the presence of pine trees? b) After the resprouting, how meristematic tissues are protected in aerial buds (terminal, axillary, and accessory) in the regenerating environment? c) Which are the adaptations of palm species that allow them to colonize and grow under areas with different disturbance histories? d) Are the palms able to resprout in the disturbed areas after the introduction of a new perturbation?

Keywords: Belowground bud bank, Resprouting strategies, Myrtaceae, Aerial buds, Accessory buds, Bud protection, Vegetative propagation, Geoxyle palms

# 1. RESPROUTING STRATEGIES OF THREE NATIVE SHRUB CERRADO SPECIES FROM A MORPHOANATOMICAL AND CHEMICAL PERSPECTIVE

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Resprouting strategies of three native shrub Cerrado species from a morphoanatomical and chemical perspective

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## 1.1. Introduction

Several ecosystems worldwide are susceptible to environmental disturbances that can interfere and modify the vegetation structure by removing or injuring the aerial organs of plants (Poorter *et al.* 2010). These disturbances, such as fire, can stimulate the development of response traits through which plants acquire resilience, inducing changes in the vegetation composition dynamics at the community level (Pausas *et al.* 2004; Poorter *et al.* 2010; Clarke *et al.* 2015). In general, changes promoted by environmental top-killing disturbances lead to two types of regeneration strategies: (i) 'seeders'– susceptible plants species that do not keep the meristematic tissues; and (ii) 'resprouters'– resilient plants species that can regenerate from protected meristematic tissues (Clarke *et al.* 2013; Pausas and Keeley 2014).

Resprouting is considered an important regenerative trait for species persistence in frequently disturbed ecosystems (Pérez-Harguindeguy *et al.* 2013). It is determined by a set of factors that include the occurrence of a viable bud bank (position and number of buds), the protection degree of buds (position and number of protective characters) and the accumulation and availability of energy resources (position and quantity) associated with the type of reserve organ (Clarke *et al.* 2013; Pausas *et al.* 2018; Klimešová *et al.* 2019). In the ‘resprouter’ plant body, the viable bud bank may be allocated in a diversity of resilient aerial organs, basal regions, belowground organs or a combination of both (Pausas *et al.* 2018; Klimešová *et al.* 2019).

The allocation of a bud bank in belowground organs is an advantageous adaptative feature of vegetation recovery (Rodrigues *et al.* 2004; de Moraes *et al.* 2016). The protection is promoted by soil, which is an effective thermal insulator (Clarke *et al.* 2013), and by protective compounds such as phenolics present in the tissues of belowground systems (da Silva *et al.* 2020), which can display defensive mechanisms such as antifungal activity, herbivory repellency, and strengthening of cell walls by providing molecules to synthesise lignin and suberin (Kulbat 2016). The diversity of belowground systems with excellent resprouting potential includes xylopodium, associated with tuberous roots (Appezzato-da-Glória and Cury 2011; Pausas *et al.* 2018), rhizomes (Konlechner *et al.* 2016; Pausas *et al.* 2018), lignotubers, and soboles (woody rhizomes) (Pausas *et al.* 2018). However, regardless of the type of organ, plants require energy for tissue development, which is mobilised from stored carbohydrates (de Moraes *et al.* 2016; de Oliveira Joaquim *et al.* 2018). These carbohydrates are usually found as glucose, fructose, sucrose, maltose, fructans and starch (de Moraes *et al.* 2016). Although their main function is to provide carbon skeletons for the formation of new aerial shoots, they also act as osmoregulators (Asega *et al.* 2011) and may protect plants against abiotic stresses (Garcia *et al.* 2011; de Oliveira Joaquim *et al.* 2018; Versluys *et al.* 2018).

The Cerrado, a phytogeographic domain, composed of tropical grasslands (campo limpo), savannas (campo sujo, campo cerrado, and cerrado sensu stricto), and seasonal forest (cerradão) (Batalha 2011), comprises disturbance-prone ecosystems, where it is possible to find several vegetative regeneration strategies (Fidelis *et al.* 2021; Pilon *et al.* 2021; Zupo *et al.* 2021). It is considered a biodiversity hotspot, with more than 7000 botanical species with high levels of endemism (Franco *et al.* 2014). Cerrado comprises the largest savanna in the neotropical region (Simon and Pennington 2012), and is characterised by the co-existence of the trees, shrubs, forbs, and grasses (Machida *et al.* 2021). The domain covers about 25% of the Brazilian territory (Durigan and Ratter 2016). However, this domain already has more than half of its area degraded (Klink and Machado 2005) due to monoculture cultivation and fire exclusion policies (Durigan and

Ratter 2016). Furthermore, the proximity of monoculture plantations to the natural areas – e.g. Pinus sp. – causes biological invasions, decreasing the richness of native species (de Abreu and Durigan 2011; de Abreu *et al.* 2011; Durigan *et al.* 2013), and its long-term presence can compromise the resilience of the entire system (Ferraro *et al.* 2020).

Phytosociological surveys in areas invaded by Pinus sp. and regenerating Cerrado areas can demonstrate the frequent occurrence of Myrtaceae species (de Abreu 2013; de Carvalho Barbosa *et al.* 2014). Myrtaceae is one of the most dominant botanical families in Cerrado vegetation, including 21 genera and more than 344 species (de Mendonça *et al.* 2008; Fiaschi and Pirani 2009). From a wide perspective, this family has one of the highest resprouting potential through belowground organs after environmental disturbances (Burrows et al. 2010; Charles-Dominique *et al.* 2015; da Silva *et al.* 2020). Although there is information about the vegetative regeneration strategies of Myrtaceae species from the Cerrado (da Silva *et al.* 2020; Pilon *et al.* 2021), little is known about the belowground bud-bearing organs which contribute to regeneration after long-term suppression due to pine cultivation (de Abreu and Durigan 2011).

Strategies of species of herbs and shrubs that use underground structures for resprouting and enable to recolonise post-fire have received considerable attention regarding plant community restoration (Pilon *et al.* 2021). Further, some methods using belowground organs fragments (Ferreira *et al.* 2015; Pilon *et al.* 2018) have been useful in savanna restoration. Since most studies on post-disturbance resprouting responses are focused on the community level (Fidelis *et al.* 2021; Pilon *et al.* 2021; Zupo *et al.* 2021), far too little attention has been paid to understand this mechanism at the species level (Appezzato-da-Glória and Cury 2011; Filartiga *et al.* 2017; da Silva *et al.* 2020). Therefore, the purpose of this survey was to investigate the belowground system of three Myrtaceae species from a morphoanatomical and chemical perspective to understand their regeneration strategy for quickly recovering a disturbed Cerrado area.

## 1.2. Further directions and conclusions

In a general context, long-term *Pinus* plantations became an issue in the Cerrado especially due to their highly invasive ability and to the development of ecological filters in the plantation sites, which drastically reduce the light availability and gradually create a thick pine needle layer over the soil (de Abreu and Durigan 2011; de Abreu *et al.* 2011). Thus, the removal of the pine trees may be helpful for the regeneration of native woody individuals, which are able to persist under the shading conditions of the understorey (Zanzarini *et al.* 2019). We hypothesised two different situations regarding the occurrence of the species: (I) these species already occurred in the former natural Cerrado area, before the establishment of the *Pinus* plantation, and fragments of their belowground organs may have survived the establishment process; or, (II) these species were introduced in the studied area, but several years ago. The evaluated belowground organs were very large, reaching more than 1 m deep, and being somewhat lignified, factors that do not match the relatively short period between the removal of the *Pinus* plantation and the resprouting of the species. Therefore, the architecture of the studied species, which involves both structural and chemical features described here, denotes an investment in protective features, which may have contributed to their endurance and survival under the *Pinus* understorey throughout the years of cultivation, being supplied by the reserves stored into the vascular parenchyma tissues of their belowground organs. However, it is of key importance that further studies should be carried out in order to estimate the age of these belowground bud-bearing organs. Moreover, the clear-cutting of *Pinus* sp. and the removal of the remaining pine biomass by fire treatment may have contributed to the development and subsequent maintenance of the belowground bud bank. Such insights are important not only to contribute to the knowledge about resprouting in general but also to understand the mechanisms that plants use to cope with disturbances in the Cerrado.

## 1.3. References

Alonso AA, Machado SR (2007) Morphological and developmental investigations of the underground system of *Erythroxylum* species from Brazilian cerrado. *Australian Journal of Botany* 55, 749–758. doi:10.1071/BT07060.

Amaral LIV, Gaspar M, Costa PMF, Aidar MPM, Buckeridge MS (2007) Novo método enzimático rápido e sensível de extração e dosagem de amido em materiais vegetais. *Hoehnea* 34, 425–431. doi:10.1590/ S2236-89062007000400001.

Angyalossy V, Pace MR, Evert RF, Marcati CR, Oskolski AA, Terrazas T, Kotina E, Lens F, Mazzoni-Viveiros SC, Angeles G, Machado SR, Crivellaro A, Rao KS, Junikka L, Nikolaeva N, Baas P (2016) IAWA list of microscopic bark features. *IAWA Journal* 37, 517–615. doi:10.1163/22941932-20160151.

Appezzato-da-Glória B (2015) ‘Morfologia de Sistemas Subterrâneos de Plantas.’ (3i Editora: Belo Horizonte, Brazil).

Appezzato-da-Glória B, Cury G (2011) Morpho-anatomical features of underground systems in six Asteraceae species from the Brazilian Cerrado. *Anais da Academia Brasileira de Ciências* 83, 981–991. doi:10.1590/S0001-37652011005000018.

Appezzato-da-Glória B, Cury G, Kasue Misaki Soares M, Rocha R, Hissae HayashiA (2008) Underground systems of Asteraceae species from the Brazilian Cerrado. *The Journal of the Torrey Botanical Society* 135, 103–113. doi:10.3159/07-RA-043.1.

Armstrong L, do Rocio Duarte M, MiguelOG (2012) Morpho-anatomy of the leaf and stem of *Eugenia pyriformis*. *Brazilian Journal of Pharmacogno*sy 22, 475–481. doi:10.1590/S0102-695X2012005000022.

Asega AF, do Nascimento JRO, Carvalho MAM (2011) Increased expression of fructan 1-exohydrolase in rhizophores of *Vernonia herbacea* during sprouting and exposure to low temperature. *Journal of Plant Physiology* 168, 558–565. doi:10.1016/j.jplph.2010.09.002.

Barbosa ACF, Pace MR, Witovisk L, Angyalossy V (2010) A new method to obtain good anatomical slides of heterogeneous plant parts. *IAWA Journal* 31, 373–383.

Batalha MA (2011) O cerrado não é um bioma. Biota Neotropica 11,21–24. doi:10.1590/S1676-06032011000100001.

Burrows GE, Chisnall LK (2016) Buds buried in bark: the reason why *Quercus suber* (cork oak) is an excellent post-fire epicormic resprouter. *Trees* 30, 241–254. doi:10.1007/s00468-015-1293-1.

Burrows GE, Hornby SK, Waters DA, Bellairs SM, Prior LD, Bowman DMJS (2010) A wide diversity of epicormic structures is present in Myrtaceae species in the northern Australian savanna biome – implications for adaptation to fire. *Australian Journal of Botany* 58, 493–507. doi:10.1071/BT10107.

Campilho A, Nieminen K, Ragni L (2020) The development of the periderm: the final frontier between a plant and its environment. *Current Opinion in Plant Biology* 53,10–14. doi:10.1016/j.pbi.2019.08.008.

Charles-Dominique T, Beckett H, Midgley GF, Bond WJ (2015) Bud protection: a key trait for species sorting in a forest-savanna mosaic. *New Phytologist* 207, 1052–1060. doi:10.1111/nph.13406.

Ciccarelli D, Garbari F, Pagni AM (2008) The flower of *Myrtus communis* (Myrtaceae): Secretory structures, unicellular papillae, and their ecological role. *Flora – Morphology, Distribution, Functional Ecology of Plants* 203,85–93. doi:10.1016/j.flora.2007.01.002.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197,19–35. doi:10.1111/nph.12001.

Clarke PJ, Lawes MJ, Murphy BP, Russell-Smith J, Nano CEM, Bradstock R, Enright NJ, Fontaine JB, Gosper CR, Radford I, Midgley JJ, Gunton RM (2015) A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of the Total Environment* 534,31–42. doi:10.1016/j.scitotenv.2015.04.002.

Corrêa Scalon M, Maia Chaves Bicalho Domingos F, Jonatar Alves da Cruz W, Marimon Júnior BH, Schwantes Marimon B, Oliveras I (2020) Diversity of functional trade-offs enhances survival after fire in Neotropical savanna species. *Journal of Vegetation Science* 31,139–150. doi:10.1111/jvs.12823.

Cruz A, Perez B, Moreno JM (2003) Resprouting of the Mediterranean-type shrub *Erica australis* with modified lignotuber carbohydrate content. *Journal of Ecology* 91, 348–356. doi:10.1046/j.1365-2745. 2003.00770.x.

da Silva GS, Ferraro A, Ogando FIB, De Aguiar CL, Appezzato-Da-Gl´oria B (2020) Structures related to resprouting potential of two Myrtaceae species from Cerrado: morpho-anatomical and chemical studies. *Anais da Academia Brasileira de Ciências* 92(1), e20180472. doi:10.1590/0001-3765202020180472.
de Abreu RCR (2013) Ecologia e controle da invasão de *Pinus elliottii* no campo cerrado. PhD thesis, Universidade de São Paulo, São Carlos, Brazil.

de Abreu RCR, de Assis GB, Frison S, Aguirre A, Durigan G (2011) Can native vegetation recover after slash pine cultivation in the Brazilian Savanna? *Forest Ecology and Management* 262, 1452–1459. doi:10.1016/j.foreco.2011.06.046.

de Abreu RCR, Durigan G (2011) Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by *Pinus elliottii* Engelm. *Plant Ecology & Diversity* 4, 269–278. doi:10.1080/ 17550874.2011.594101.

de Antonio AC, Scalon MC, Rossatto DR (2020) The role of bud protection and bark density in frost resistance of savanna trees. *Plant Biology* 22, 55–61. doi:10.1111/plb.13050.

de Campos BH, Guimarães E, Canaveze Y, Machado SR (2021) Epicormic bud protection traits vary along a latitudinal gradient in a neotropical savanna. *The Science of Nature* 108, 11. doi:10.1007/s00114-02101722-4.

de Carvalho Barbosa B, Siqueira Cappi V, Pontes Ribeiro S, Wilson Fernandes G (2014) Avaliação da capacidade de rebrotamento pós distúrbio das plantas lenhosas típicas dos campos rupestres. *Ecología Austral* 24, 350–355. doi:10.25260/EA.14.24.3.0.13.

de Mendonça RC, Felfili JM, Walter BMT, daJúnior MCS, Rezende AV, deFilgueiras TS, Nogueira PE, Fagg CW (2008) Flora vascular do bioma Cerrado. In ‘Cerrado: ecologia e flora’. (Eds SM Sano, SP de Almeida, JF Ribeiro) pp. 1028–1059. (Embrapa: Brasília, Brazil).

de Moraes MG, de Carvalho MAM, Franco AC, Pollock CJ, Figueiredo-Ribeiro RDCL (2016) Fire and drought: soluble carbohydrate storage and survival mechanisms in herbaceous plants from the Cerrado. *BioScience* 66, 107–117. doi:10.1093/biosci/biv178.

de Oliveira Joaquim E, Moura Silva T, Leone Figueiredo-Ribeiro RC, de Moraes MG, de Carvalho MAM (2018) Diversity of reserve carbohydrates in herbaceous species from Brazilian campo rupestre reveals similar functional traits to endure environmental stresses. *Flora* 238, 201–209. doi:10.1016/j.flora.2017.01.001.

Diaz-Toribio MH, Putz FE (2021) Underground carbohydrate stores and storage organs in fire-maintained longleaf pine savannas in Florida, USA. *American Journal of Botany* 108,432–442. doi:10.1002/ajb2.1620.

DuBois M, Gilles KA,Hamilton JK, Rebers PAT, Smith F (1956) Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28, 350–356. doi:10.1021/ac60111a017.

Durigan G, Ivanauskas NM, Zakia MJB, de Abreu RCR (2013) Control of invasive plants: ecological and socioeconomic criteria for the decision making process. *Natureza & Conservação* 11,23–30. doi:10.4322/ natcon.2013.003.

Durigan G, Ratter JA (2016) The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology* 53,11–15. doi:10.1111/1365-2664.12559.

Ferraro A, Fidelis A, da Silva GS, Martins AR, Piedade SMDS, Appezzato-da-Glória B (2020) Long-term *Pinus* plantations reduce the bud bank in Cerrado areas. *Applied Vegetation Science* 24, e12537. doi:10.1111/ avsc.12537.

Ferraz A, Mendonça R, da Silva FT (2000) Organosolv delignification of white-and brown-rotted *Eucalyptus grandis* hardwood. *Journal of Chemical Technology & Biotechnology* 75,18–24. doi:10.1002/(SICI) 1097-4660(200001)75:1<18::AID-JCTB169>3.0.CO;2-Z.

Ferreira MC, Walter BMT, Vieira DLM (2015) Topsoil translocation for Brazilian savanna restoration: propagation of herbs, shrubs, and trees. *Restoration Ecology* 23, 723–728. doi:10.1111/rec.12252.

Fiaschi P, Pirani JR (2009) Review of plant biogeographic studies in Brazil. *Journal of Systematics and Evolution* 47, 477–496. doi:10.1111/ j.1759-6831.2009.00046.x.

Fidelis A, Rodrigues CA, Dairel M, Blanco CC, Pillar VD, Pfadenhauer J (2021) What matters for vegetation regeneration in Brazilian subtropical grasslands: seeders or resprouters? *Flora* 279, 151817. doi:10.1016/j.flora.2021.151817.

Filartiga AL, Klimešová J, Appezzato-da-Glória B (2017) Underground organs of Brazilian Asteraceae: testing the CLO-PLA database traits. *Folia Geobotanica* 52, 367–385. doi:10.1007/s12224-016-9266-8.

Franceschi VR, Krokene P, Christiansen E, Krekling T (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167, 353–376. doi:10.1111/j.1469-8137.2005. 01436.x.

Franceschi VR, Nakata PA (2005) Calcium oxalate in plants: formation and function. *Annual Review of Plant Biology* 56,41–71. doi:10.1146/ annurev.arplant.56.032604.144106.

Franco AC, Rossatto DR, de Carvalho Ramos Silva L, da Silva Ferreira C (2014) Cerrado vegetation and global change: the role of functional types, resource availability and disturbance in regulating plant community responses to rising CO2 levels and climate warming. *Theoretical and Experimental Plant Physiology* 26,19–38. doi:10.1007/ s40626-014-0002-6.

Garcia PMA, Asega AF, Silva EA, Carvalho MAM (2011) Effect of drought and re-watering on fructan metabolism in *Vernonia herbacea* (Vell.) Rusby. *Plant Physiology and Biochemistry* 49, 664–670. doi:10.1016/ j.plaphy.2011.03.014.

Gerlach D (1984) ‘Botanische Mikrotechnik.’ (Georg Thieme Verlag: New York, NY, USA).

Jagiełło R, Baraniak E, Guzicka M, Karolewski P, Łukowski A, Giertych MJ (2019) One step closer to understanding the ecology of *Cameraria ohridella* (Lepidoptera: Gracillariidae): The effects of light conditions. *European Journal of Entomology* 116,42–51. doi:10.14411/ EJE.2019.005.

Jeník J (1994) Clonal growth in woody plants: a review. *Folia Geobotanica et Phytotaxonomica* 29, 291–306. doi:10.1007/BF02803802.

Jensen WA (1962) ‘Botanical histochemistry: principles and practice.’(W.H. Freeman: San Francisco, CA, USA).

Johansen DA (1940) ‘Plant microtechnique.’ (McGraw-Hill Book Company: New York, NY, USA).

Klimešová J, Martínková J, Herben T (2018) Horizontal growth: an overlooked dimension in plant trait space. *Perspectives in Plant Ecology, Evolution and Systematics* 32,18–21. doi:10.1016/j.ppees.2018.02.002.

Klimešová J, Martínková J, Pausas JG, de Moraes MG, Herben T, Yu FH, Puntieri J, Vesk PA, de Bello F, Janeček Š, Altman J, Appezzato-da-Glória B, Bartušková A, Crivellaro A, Doležal J, Ott JP, Paula S, Schnablová R, Schweingruber FH, Ottaviani G (2019) Handbook of standardized protocols for collecting plant modularity traits. *Perspectives in Plant Ecology, Evolution and Systematics* 40, 125485. doi:10.1016/j.ppees.2019.125485.

Klink CA, Machado RB (2005) A conservação do Cerrado brasileiro. *Megadiversidade* 1, 147–155. doi:10.1590/S0100-69912009000400001.

Konlechner TM, Orlovich DA, Hilton MJ (2016) Restrictions in the sprouting ability of an invasive coastal plant, *Ammophila arenaria*, from fragmented rhizomes. *Plant Ecology* 217, 521–532. doi:10.1007/ s11258-016-0597-6.

Kulbat K (2016) The role of phenolic compounds in plant resistance. *Biotechnology and Food Sciences* 80,97–108. Available at http:// www.bfs.p.lodz.pl.

Lanoue A, Burlat V, Schurr U, Röse USR (2010) Induced root-secreted phenolic compounds as a belowground plant defense. *Plant Signaling & Behavior* 5, 1037–1038. doi:10.4161/psb.5.8.12337.

Lattanzio V, Lattanzio VMT, Cardinali A (2006) Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. In ‘Phytochemistry: advances in research’. (Ed. F Imperato) pp. 23–67. (Research Signpost: Trivandrum, Kerala, India).

Luque R, de Sousa HC, Kraus JE (1996) Métodos de coloração de Roeser (1972): modificado – e Kropp (1972) visando a substituição do azul de astra por azul de alcião 8GS ou 8GX. *Acta Botanica Brasilica* 10, 199–212. doi:10.1590/S0102-33061996000200001.

Machida WS, Gomes L, Moser P, Castro IB, Miranda SC, da Silva-Júnior MC, Bustamante MMC (2021) Long term post-fire recovery of woody plants in savannas of central Brazil. *Forest Ecology and Management* 493, 119255. doi:10.1016/j.foreco.2021.119255.

Meira Neto JAA, Martins FR, Valente GE (2007) Composição florística e espectro biológico na Estação Ecológica de Santa Bárbara, estado de São Paulo, Brasil. *Revista Árvore* 31, 907–922. doi:10.1590/S010067622007000500015.

Melo ACG, Durigan G (2011) ‘Plano de manejo da Estação Ecológica de Santa Bárbara.’ (Instituto Florestal/SEMA: São Paulo, Brazil).

Nakata PA (2003) Advances in our understanding of calcium oxalate crystal formation and function in plants. *Plant Science* 164, 901–909. doi:10.1016/S0168-9452(03)00120-1.

Nakata PA (2012) Plant calcium oxalate crystal formation, function, and its impact on human health. *Frontiers in Biology* 7, 254–266. doi:10.1007/s11515-012-1224-0.

Oborny B, Mony C, Herben T (2012) From virtual plants to real communities: a review of modelling clonal growth. *Ecological Modelling* 234,3–19. doi:10.1016/j.ecolmodel.2012.03.010.

Ott JP, Klimešová J, Hartnett DC (2019) The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123, 1099–1118. doi:10.1093/aob/mcz051.

Ottaviani G, Molina-Venegas R, Charles-Dominique T, Chelli S, Campetella G, Canullo R, Klimešová J (2020) The neglected belowground dimension of plant dominance. *Trends in Ecology & Evolution* 35, 763–766. doi:10.1016/j.tree.2020.06.006.

Paula S, Naulin PI, Arce C, Galaz C, Pausas JG (2016) Lignotubers in Mediterranean basin plants. *Plant Ecology* 217,661–676. doi:10.1007/ s11258-015-0538-9.

Pausas JG, Bradstock RA, Keith DA, Keeley JE (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85, 1085– 1100. doi:10.1890/02-4094.

Pausas JG, Keeley JE (2014) Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204,55–65. doi:10.1111/nph.12921.

Pausas JG, Keeley JE (2017) Epicormic resprouting in fire-prone ecosystems. *Trends in Plant Science* 22, 1008–1015. doi:10.1016/ j.tplants.2017.08.010.

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A (2018) Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* 217, 1435–1448. doi:10.1111/nph.14982.

Pearse AGE (1968) 'Histochemistry: theoretical and applied.' (J. & A. Churchill Ltd: London, UK).
Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 64(3), 167–234. doi:10.1071/BT12225.

Pilon NAL, Buisson E, Durigan G (2018) Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. *Restoration Ecology* 26,73–81. doi:10.1111/rec.12534.

Pilon NAL, Cava MGB, Hoffmann WA, Abreu RCR, Fidelis A, Durigan G (2021) The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology* 109, 154–166. doi:10.1111/ 1365-2745.13456.

Poorter L, Kitajima K, Mercado P, Chubi˜J, Melgar I, Prins HHT na (2010) Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology* 91, 2613–2627. doi:10.1890/09-0862.1.

Purrington CB (2000) Costs of resistance. Current Opinion in Plant Biology 3, 305–308. doi:10.1016/S1369-5266(00)00085-6.

Raunkiaer C (1934) 'The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer.' (Clarendon Press: Oxford, UK).

Rocha LD, Preussler KH, Pegorini F, de Farias V,Maranho LT (2008) Estudo anatômico comparativo da casca do caule do araçá-amarelo e araçávermelho, *Psidium cattleianum* Sabine, Myrtaceae. *Acta Botanica Brasilica* 22,1114–1122. doi:10.1590/s0102-33062008000400022.

Rodrigues RR, Torres RB, Matthes LAF, Penha AS (2004) Tree species sprouting from root buds in a semideciduous forest affected by fires. *Brazilian Archives of Biology and Technology* 47, 127–133. doi:10.1590/S1516-89132004000100017.

Silva SP, Sabino MA, Fernandes EM, Correlo VM, Boesel LF, Reis RL (2005) Cork: properties, capabilities and applications. *International Materials Reviews* 50, 345–365. doi:10.1179/174328005X41168.

Simon MF, Pennington T (2012) Evidence for adaptation to fire regimes in the tropical Savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* 173, 711–723. doi:10.1086/665973.

Soffiatti P, Angyalossy-Alfonso V (1999) Estudo anatômico comparativo do lenho e da casca de duas espécies de *Eugenia* L. (Myrtaceae). Revista Brasileira de Botânica 22, 175–184. doi:10.1590/S0100-840419 99000200008.

Soliman S, Mohammad MG, El-Keblawy AA, Omar H, Abouleish M, Madkour M, Elnaggar A, Hosni RM (2018) Mechanical and phytochemical protection mechanisms of *Calligonum comosum* in arid deserts. *PLoS One* 13, e0192576. doi:10.1371/journal.pone.0192576.

Storey R, Wyn Jones RG, Schachtman DP, Treeby MT (2003) Calcium-accumulating cells in the meristematic region of grapevine root apices. *Functional Plant Biology* 30, 719–727. doi:10.1071/FP02212.

Strasburger E (1913) ‘Handbook of practical botany.’ (George Allen & Company Ltda: London, UK).

Verdaguer D(2020) Towards a better understanding of the role of rhizomes in mature woody plants: the belowground system of *Quercus coccifera*. *Trees* 34,903–916. doi:10.1007/s00468-020-01969-w.

Vergílio PCB, Marcati CR (2017) Adaptive and diagnostic significance of the bark of *Stryphnodendron polyphyllum* (Leguminosae) from the Cerrado. *Australian Journal of Botany* 65, 157–171. doi:10.1071/ BT16212.

Versluys M, Kirtel O, Toksoy Öner E, Van den Ende W(2018) The fructan syndrome: evolutionary aspects and common themes among plants and microbes. *Plant Cell and Environment* 41,16–38. doi:10.1111/ pce.13070.

Zanzarini V, Zanchetta D, Fidelis A (2019) Do we need intervention after pine tree removal? The use of different management techniques to enhance Cerrado natural regeneration. *Perspectives in Ecology and Conservation* 17, 146–150. doi:10.1016/j.pecon.2019.07.001.

Zupo T, Daibes LF, Pausas JG, Fidelis A (2021) Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science* 32, e12968. doi:10.1111/jvs.12968.

# 2. ANATOMICAL INFERENCES ON AERIAL BUD PROTECTION OF THREE *Eugenia* SHRUB SPECIES FROM CERRADO

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**Anatomical inferences on aerial bud protection of three**
***Eugenia* shrub species from Cerrado**

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## 2.1. Introduction

Seasonal or occasional environmental disturbances, caused either by natural or anthropic actions, remove the aerial organs of plants. In disturbance-prone areas, the capacity of plant species to regenerate and spread vegetatively play a crucial role in the recovery of the ecosystem (Pilon *et al*. 2021). In general, plants can allocate buds and regenerate from a variety of organs (Pausas *et al*. 2018). Nonetheless, in domains such as Cerrado, the world's most species-rich tropical savanna with high levels of endemism (Simon *et al*. 2009), the allocation of buds occurs mainly in belowground structures (Ottavianni *et al*. 2020), while several strategies are adopted to restore the aboveground biomass at the community (Pilon *et al*. 2021) and species levels (Silva *et al*. 2021; Ferraro *et al*. 2021).

The aboveground buds have been receiving special attention lately due to the importance that they represent in the recovery and resilience of the vegetation after a disturbance (Charles-Dominique *et al*. 2015; Corrêa-Scalon *et al*. 2020; de Antonio *et al*. 2020, 2021). Following resprouting, plants need to restore the reserves consumed to form new aboveground biomass (de Carvalho Barbosa *et al*. 2014; Moreira *et al*. 2012). In this sense, the protection of the terminal and axillary buds is important in the vegetation re-establishment since these buds are responsible to form new photosynthetic tissues for the plants to grow.

In trees, the protection of buds is related to the bark, which is a well-studied trait involved in aerial bud protection (Burrows & Chisnall 2016; Charles-Dominique *et al.* 2015; Clarke *et al.* 2013; de Antonio *et al.* 2020). However, only the bark thickness is not strictly related to a higher degree of protection, but a combination of bark features and the location of the buds on the stem (e.g. fully exposed, in bark depressions) (de Antonio *et al.* 2021) and the presence of trichomes, in the case of fire-prone species, are in fact effective in the bud protection (Chiminazzo *et al.* 2021).

In species with aerial buds not covered or related to the bark, the buds can be well protected by structural and chemical features (de Campos *et al.* 2021; da Silva *et al.* 2020). In Terminal, axillary and accessory buds, species can be protected by the base of the corresponding leaf (Bell *et al.* 1999), by stipules and cataphylls (de Campos *et al.* 2021). These aerial buds can also develop protective structures against biotic and abiotic stressors such as trichomes containing phenolic compounds (Burrows 2008; de Campos *et al.* 2021; Karabourniotis *et al.* 2020b; da Silva *et al.* 2020), thick cuticle in the leaf primordia, colleters, crystals idioblasts, phenolic idioblasts, sclereids, and oil cavities (da Silva *et al.* 2020).

The Cerrado thrives in a region exposed to high irradiances, dry cool winter months when fire events frequently occur, high atmospheric evaporative demand, and low relative humidity (Franco *et al.* 2014). Frost is an important cause of top-kill and plant damage in the southern limits of the Cerrado and at higher elevation sites (Brando & Durigan 2004; De Antonio *et al.* 2020). Most studies on bud protection traits in the Cerrado have investigated their role in enhancing plant persistence in response to these environmental disturbances with a focus on trees (Chiminazzo *et al.* 2021; de Antonio *et al.* 2020, 2021; de Campos *et al.* 2021). But several species from the herbaceous-shrubby layer show distinct responses to frost and some of them are not damaged (Pilon 2019). However, the features that are protecting the aerial buds in herbaceous-shrubby species are barely investigated so far (da Silva *et al.* 2020).

Since bud protection plays a crucial role in the re-establishment of Cerrado vegetation after disturbances, this study evaluates how meristematic tissues are protected in aerial buds (terminal, axillary, and accessory) of three *Eugenia* shrub species. All collected individuals were fully exposed to sunlight since they resprouted in an open Cerrado area, which is under regeneration after long-term pine cultivation. We hypothesized that the aerial buds are highly protected to ensure plant growth and resilience in this regenerating area. We expect with this detailed anatomical study of aerial buds to bring new knowledge yet rarely explored for bud protection studies, especially in the herbaceous-shrubby layer.

## 2.2. Conclusions

Our finds demonstrate that the structural and chemical bud features, along with the combination of axillary and accessory buds contribute to the survival and persistence of these shrub species subject to environmental disturbances such as frost events during the dry period of the year (from June to August) and the full exposure to sunlight in a regenerating ecosystem. Since the aerial buds of all studied species are not protected by bark, they are not correctly fitted into the bud protection classifications available in the literature that are made for trees. Therefore, it is evident that the classification of aerial bud protection needs to be expanded to include anatomical and chemical features as well as species from the herbaceous-shrub layer that are subject to biotic and abiotic stressors.

## 2.3. References

Almeida, A.L., Paiva, E.A.S. (2019) Colleters in *Mabea fistulifera* Mart. (Euphorbiaceae): Anatomy and biology of the secretory process. *Flora*, **258**, 151439.

Ballego-Campos, I., Paiva, É. A. S. (2018) Mucilage secretion in the inflorescences of *Aechmea blanchetiana*: Evidence of new functions of scales in Bromeliaceae. *Flora*, **246**, 1-9.

Bell, A.D., Bell, A., Dines, T.D. (1999) Branch construction and bud defence status at the canopy surface of a West African rainforest. *Biological Journal of the Linnean Society*, **66**, 481–499.

Brando, P. M., Durigan, G. (2005). Changes in cerrado vegetation after disturbance by frost (São Paulo State, Brazil). *Plant Ecology*, **175**, 205-215.

Burrows, G.E. (2008) *Syncarpia* and *Tristaniopsis* (Myrtaceae) possess specialised fire-resistant epicormic structures. *Australian Journal of Botany*, **56**, 254–264.

Burrows, G. E. (2013) Buds, bushfires and resprouting in the eucalypts. *Australian Journal of Botany*, **61**, 331-349.

Burrows, G.E., Chisnall, L.K. (2016) Buds buried in bark: the reason why *Quercus suber* (cork oak) is an excellent post-fire epicormic resprouter. *Trees*, **30**, 241–254.

Burrows, G.E., Hornby, S.K., Waters, D.A., Bellairs, S.M., Prior, L.D., Bowman, D.M.J.S. (2010) A wide diversity of epicormic structures is present in Myrtaceae species in the northern Australian savanna biome implications for adaptation to fire. *Australian Journal of Botany,* **58**, 493–507.

Burrows, G.E., Hornby, S.K., Waters, D.A., Bellairs, S.M., Prior, L.D., Bowman, D.M.J.S. (2008) Leaf axil anatomy and bud reserves in 21 Myrtaceae species from Northern Australia. *International Journal of Plant Sciences*, **169**, 1174–1186.

Cain, A.J. (1947) The use of Nile blue in the examination of lipoids. *Journal of Cell Science*, **s3-88**, 383–392.

Castro, M. D. M., Demarco, D. (2008) Phenolic compounds produced by secretory structures in plants: a brief review. *Natural Product Communications,* **3**, 1273-1284.

Castro Miguel, E., Klein, D.E., de Oliveira, M.A., da Cunha, M. (2010) Ultrastructure of secretory and senescence phase in colleters of *Bathysa gymnocarpa* and *B. stipulata* (Rubiaceae). *Brazilian Journal of Botany*, **33**, 425-436.

Ciccarelli, D., Garbari, F., Pagni, A.M. (2008) The flower of *Myrtus communis* (Myrtaceae): Secretory structures, unicellular papillae, and their ecological role. *Flora*, **203**, 85–93.

Charles-Dominique, T., Beckett, H., Midgley, G.F., Bond, W.J. (2015) Bud protection: A key trait for species sorting in a forest-savanna mosaic. *New Phytologist*, **207**, 1052–1060.

Chiminazzo, M.A., Bombo, A.B., Charles-Dominique, T., Fidelis, A. (2021) Your best buds are worth protecting: Variation in bud protection in a fire-prone cerrado system. *Functional Ecology,* **231**, 1278-1295.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E. (2013) Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist*, **197**, 19–35.

Corrêa-Scalon, M., Maia Chaves Bicalho Domingos, F., Jonatar Alves da Cruz, W., Marimon Júnior, B.H., Schwantes Marimon, B., Oliveras, I. (2020) Diversity of functional trade-offs enhances survival after fire in Neotropical savanna species. *Journal of Vegetation Science,* **31**, 139–150.

Costa, I.S.C., Lucena, E.M.P., Bonilla, O.H., Guesdon, I.R., Coutinho, Í.A.C. (2020) Seasonal variation in colleter exudates in *Myrcia splendens* (Myrtaceae). *Australian Journal of Botany,* **68**, 403.

da Silva, C.J., Barbosa, L.C.A., Marques, A.E., Baracat-Pereira, M.C., Pinheiro, A.L., Meira, R.M.S.A. (2012) Anatomical characterization of the foliar colleters in Myrtoideae (Myrtaceae). *Australian Journal of Botany,* **60**, 707.

de Abreu, R.C.R., Durigan, G. (2011) Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by *Pinus elliottii* Engelm. *Plant Ecology & Diversity*, **4**, 269–278.

de Antonio, A.C., Scalon, M.C., Rossatto, D.R. (2020) The role of bud protection and bark density in frost resistance of savanna trees. *Plant Biology*, **22**, 55–61.

de Antonio, A.C., Hoffmann, W.A., Rossatto, D.R. (2021) The role of morphophysiological traits in frost tolerance of neotropical savanna trees. *Trees*, **35**, 1687-1696.

de Campos, B.H., Guimarães, E., Canaveze, Y., Machado, S.R. (2021) Epicormic bud protection traits vary along a latitudinal gradient in a neotropical savanna. *Naturwissenschaften*, **108**, 11.

de Carvalho Barbosa, B., Siqueira Cappi, V., Pontes Ribeiro, S., Wilson Fernandes, G. (2014) Avaliação da capacidade de rebrotamento pós distúrbio das plantas lenhosas típicas dos campos rupestres. *Ecología Austral*, **24**, 350–355.

Durigan, G., Pilon, N.A.L., Assis, G.B., Souza, F.M., Baitello, J.B. (2018). *Plantas pequenas do cerrado: biodiversidade negligenciada*. Governo do Estado de São Paulo, Secretaria do Meio Ambiente, Instituto Florestal, São Paulo, BR: 720 p.

Fernandez-Marín, B., Hernández, A., Garcia-Plazaola, J.I., Esteban, R., Miguez, F., Artetxe, U., Gómez-Sagasti, M.T. (2017) Photoprotective strategies of Mediterranean plants in relation to morphological traits and natural environment pressure: A meta-analytical approach. *Frontiers in Plant Sciences*, **8**, 1-16.

Ferraro, A., Fidelis, A., da Silva, G.S., Martins, A.R., Piedade, S.M.D.S., Appezzato-da-Glória, B. (2020) Long-term *Pinus* plantations reduce the bud bank in Cerrado areas. *Applied Vegetation Science*, **24**, e12537.

Ferraro, A., da Silva, G.S., de Aguiar, C.L., Appezzato-da-Glória, B. (2021) Evaluating belowground bud banks of native species from Cerrado: Structural, chemical, and ecological approaches. *Flora*, **281**, 151852.

Franceschi, V.R., Krokene, P., Krekling, T., Christiansen, E. (2000) Phloem parenchyma cells are involved in local and distant defense responses to fungal inoculation or bark-beetle attack in Norway spruce (Pinaceae). *American Journal of Botany*, **87**, 314–326.

Franco, A. C., Rossatto, D. R., de Carvalho Ramos Silva, L., da Silva Ferreira, C. (2014). Cerrado vegetation and global change: the role of functional types, resource availability and disturbance in regulating plant community responses to rising CO2 levels and climate warming. *Theoretical and Experimental Plant Physiology*, **26**, 19-38.

Gregory, M., Baas, P. (1989) A survey of mucilage cells in vegetative organs of the Dicotyledons. *Israel Journal of Botany*, **38**, 125–174.

Haddad, T.M., Pilon, N.A.L., Durigan, G., Viani, R.A.G. (2021) Restoration of the Brazilian savanna after pine silviculture: Pine clearcutting is effective but not enough. *Forest Ecology and Management*, **491**, 119158.

Horridge, G.A., Tamm, S.L. (1969) Critical point drying for scanning electron microscopic study of ciliary motion. *Science*, **163**, 817–818.

Hudgins, J.W., Krekling, T., Franceschi, V.R. (2003) Distribution of calcium oxalate crystals in the secondary phloem of conifers: a constitutive defense mechanism? *New Phytologist*, **159**, 677–690.

Jensen, W.A. (1962) Botanical histochemistry: Principles and Practice. W. H. Freeman, San Francisco, USA: 408 p.

Johansen, D.A. (1940) Plant Microtechnique. McGraw-Hill Book Company Inc., London, UK: 523 pp.

Karabourniotis, G., Horner, H.T., Bresta, P., Nikolopoulos, D., Liakopoulos, G. (2020a) New insights into the functions of carbon–calcium inclusions in plants. *New Phytologist*, **228**, 845–854.

Karabourniotis, G., Liakopoulos, G., Nikolopoulos, D., Bresta, P. (2020b) Protective and defensive roles of non-glandular trichomes against multiple stresses: structure–function coordination. *Journal of Forestry Research*, **31**, 1-12.

Karnovsky, M.J. (1965) A formaldehyde glutaraldehyde fixative of high osmolality for use in electron microscopy. *Journal of Cell Biology,* **27,** 1A-149A.

Klink, C.A., Machado, R.B. (2005) A conservação do Cerrado brasileiro. *Megadiversidade*, **1**, 147–155.

Lev-Yadun, S. (2007) Defensive functions of white coloration in coastal and dune plants. *Israel Journal of Plant Sciences*, **54**, 317–325.

McManus, J.F.A. (1948) Histological and Histochemical Uses of Periodic Acid. *Stain Technology*, **23**, 99–108.

Mercadante-Simões, M.O., Paiva, E.A.S. (2013) Leaf colleters in *Tontelea micrantha* (Celastraceae, Salacioideae): Ecological, morphological and structural aspects. *Comptes Rendus Biologies,* **336**, 400–406.

Moles, A.T., Laffan, S.W., Keighery, M., Dalrymple, R.L., Tindall, M.L., Chen, S. (2020) A hairy situation: Plant species in warm, sunny places are more likely to have pubescent leaves. *Journal of Biogeography*, **47**, 1934–1944.

Moreira, B., Tormo, J., Pausas, J.G. (2012) To resprout or not to resprout: Factors driving intraspecific variability in resprouting. *Oikos*, **121**, 1577–1584.

Nakata, P.A. (2003) Advances in our understanding of calcium oxalate crystal formation and function in plants. *Plant Science*, **164**, 901–909.

Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., Klimešova, J. (2020) The neglected belowground dimension of plant dominance. *Trends in Ecology & Evolution*, 35, 763–766.

Paiva, E.A.S. (2019) Are calcium oxalate crystals a dynamic calcium store in plants? *New Phytologist*, **223**, 1707–1711.

Pausas, J.G., Lamont, B.B., Paula, S., Appezzato-da-Glória, B., Fidelis, A. (2018) Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist*, **217**, 1435–1448.

Pearse, A.G.E. (1968) Histochemistry: Theoretical and Applied. J. & A. Churchill Ltd., London, UK: 456 pp.

Pilon, N.A.L. (2019) Efeitos de distúrbios naturais e da supressão do fogo na diversidade e estrutura do estrato herbáceo-arbustivo do Cerrado. Thesis, University of Campinas, São Paulo State, Brazil: 170 pp.

Pilon, N.A.L., Buisson, E., Durigan, G. (2018) Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. *Restoration Ecology*, **26**, 73–81.

Pilon, N.A.L., Cava, M. G., Hoffmann, W. A., Abreu, R. C., Fidelis, A., Durigan, G. (2021). The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology*, **109**, 154-166.

Rasband, W.S., 2006. Image J. National Institute of Health. Bethesda.

Reynolds, E.S. (1963) The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *Journal of Cell Biology*, **17**, 208–212.

Ribeiro, J.C., Ferreira, M.J.P., Demarco, D. (2017) Colleters in Asclepiadoideae (Apocynaceae): protection of meristems against desiccation and new functions assigned. *International Journal of Plant Sciences*, **178**, 465–477.

Sakai, W.S. (1973) Simple method for differential staining of paraffin embedded plant material using toluidine blue O. *Stain Technology*, **48**, 247–249.

Silva, M. dos S., Coutinho, Í.A.C., Araújo, M.N., Meira, R.M.S.A. (2017) Colleters in *Chamaecrista* (L.) Moench sect. *Chamaecrista* and sect. *Caliciopsis* (Leguminosae-Caesalpinioideae): anatomy and taxonomic implications. *Acta Botanica Brasilica*, **31**, 382–391.

Silva, G.S., Ferraro, A., de Aguiar, C.L., Appezzato-Da-Glória, B. (2021) Resprouting strategies of three native shrub Cerrado species from a morphoanatomical and chemical perspective. *Australian Journal of Botany*, **69**, 527-542.

Silva, G.S., Ferraro, A., Ogando, F.I.B., de Aguiar, C.L., Appezzato-Da-Glória, B. (2020) Structures related to resprouting potential of two Myrtaceae species from Cerrado: Morpho-anatomical and chemical studies. *Anais da Academia Brasileira de Ciências*, **92**, 1–18.

Simon, M. F., Grether, R., de Queiroz, L. P., Skema, C., Pennington, R. T., Hughes, C. E. (2009). Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences, 106 (48), 20359-20364.

Simon, M.F., Pennington, T. (2012) Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences*, **173**, 711–723.

Sobral, M., Proença, C., Souza, M., Mazine, F., Lucas, E. (2015) *Myrtaceae* in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available in <http://floradobrasil2015.jbrj.gov.br/jabot/floradobrasil/FB31513>.

Schoonderwoerd, K.M., Friedman, W.E. (2021) Naked resting bud morphologies and their taxonomic and geographic distributions in temperate, woody floras. *New Phytologist*, **232**, 523-536.

Soliman, S., Mohammad, M.G., El-Keblawy, A.A., Omar, H., Abouleish, M., Madkour, M., Elnaggar, A., Hosni, R.M. (2018) Mechanical and phytochemical protection mechanisms of *Calligonum comosum* in arid deserts. *PLoS ONE*, **13**, 1–15.

Tian, D., Tooker, J., Peiffer, M., Chung, S. H., Felton, G. W. (2012) Role of trichomes in defense against herbivores: comparison of herbivore response to woolly and hairless trichome mutants in tomato (*Solanum lycopersicum*). *Planta*, **236**, 1053-1066.

Tozin, L.R.S., de Melo Silva, S.C., Rodrigues, T.M. (2016) Non-glandular trichomes in Lamiaceae and Verbenaceae species: morphological and histochemical features indicate more than physical protection. *New Zealand Journal of Botany*, **54**, 446–457.

Vidal, B.C. (1970) Dichroism in collagen bundles stained with xylidine Ponceau 2R. *Annales d'histochimie*, 15, 289–296.

Wang, X., Shen, C., Meng, P., Tan, G., Lv, L. (2021). Analysis and review of trichomes in plants. *BMC plant biology*, 21(1), 1-11.

# 3. ACAULESCENT PALMS ARE HIGHLY RESILIENT TO DISTURBANCES

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## 3.1. Introduction

Acaulescence (trunkless) is an ecologically and evolutionary important growth form in plants (Tribble *et al.* 2021). As they maintain their continued growth belowground, acaulescent species increase their chances of survival following disturbances such as frequent fires (Cássia-Silva *et al.* 2022). By using the reserve energy stored belowground, they can regenerate the aerial biomass in favorable conditions (Alonso and Machado 2007; Appezzato-da-Glória 2015).

About 250 of the 2,585 described palm species (Palmweb 2022) are acaulescent (Quattrocchi 2018) with belowground stems (i.e., rhizomes). Acaulescent palm lineages are scattered across the palm phylogeny (Kissling *et al.* 2019) and show higher speciation rates than non-acaulescent lineages. This high diversification is related to an evolutionary transition to seasonally dry habitats (Cássia-Silva *et al.* 2022). Among the suite of speciation traits displayed by palms, the ramification of rhizomes after disturbances is considered one of the most important adaptive features. Species such as *Allagoptera arenaria*, for example, can ramify the main belowground axis and form clustering rhizomes (Menezes and Araujo 2004). This branching pattern of the rhizome provides an important role in the competition, nutrient acquisition, reproduction and resprouting after a disturbance (Klimešová *et al.* 2019). In Neotropical palms, the belowground stem with great amount of water and carbohydrate storage is considered a preadaptation by which rainforest lineages were able to colonize and diversify in new disturbance-prone environments (Cássia-Silva *et al.* 2022). However, very little is known about the biology of acaulescent palms, and specially about their response to disturbances.

Disturbances are common phenomena that occur in ecosystems worldwide and dynamically shape vegetation. Current disturbances include natural (e.g. fire, wind, frost, drought, hurricanes, storms) (Foster et al. 1999; Gregow *et al.* 2017; Hoffmann *et al.* 2019; Zeppel *et al.* 2015; Zupo *et al.* 2021) and human-induced processes (e.g. alien species cultivation, deforestation, harvesting) (Endress *et al.* 2004; Montúfar *et al.* 2011; Zanzarini *et al.* 2019). Disturbances, whether natural or anthropogenic, affect aerial biomass; they can select distinct plant resilience strategies and shape the functional composition of communities (Dantas *et al.* 2013, 2016; Łaska 2001; Poorter *et al.* 2010). Regarding the resilience strategies, the resprouting ability has been considered one of the primary response traits in the rapid recovery of vegetation after disturbances (Clarke *et al.* 2013; Zeppel *et al.* 2015), because it enables the formation of new shoots after the destruction of aerial organs allowing the survival of individuals (Pausas *et al.* 2015).

Resprouting depends on the combination of a viable bud bank and the availability of energy resources stored in surviving tissues (Clarke *et al.* 2013; Vesk and Westoby 2004). The bud's functionality, however, depends on their age, size, type, location (Ott *et al.* 2019), disturbances regime, and other biotic and abiotic factors that collectively regulate bud bank performance (Bombo *et al.* 2022; Ferraro *et al.* 2020). A viable bud bank can be located in aerial stems, which it usually occurs in woody species (Charles-Dominique *et al.* 2015; Chiminazzo *et al.* 2021; De Antonio *et al.* 2020), basal regions, and in a variety of belowground systems (where buds are well protected by the soil) such as rhizomes, xylopodia and gemiferous roots, or in a combination of both above- and belowground organs (Pausas *et al.* 2018).

This study aimed to investigate the resilience of acaulescent palms to disturbances. Specifically, we studied the response to anthropogenic disturbances of two acaulescent palm species from the Brazilian Cerrado with different habits: *Allagoptera campestris* (solitary) and *Syagrus loefgrenii* (clustering). We first studied populations of those palms with different disturbance history that include pine cultivation in the Cerrado and the elimination of the pines (Cerrado restoration).  Then, in the same populations, we clear-cut the palms and monitored their response (e.g., resprouting) hypothesizing that only the plants from the undisturbed area can recover properly after clear-cutting. Furthermore, we compiled a global database on acaulescent palms from published literature to understand what is known about the response to disturbances in acaulescent palms.

## 3.2. Conclusions

The native acaulescent palm species are capable of altering their morphological traits to deal with a disturbed environment. Even though the features of soil are altered both under the cultivation of pine trees and in the regenerating area, we have shown that not only aboveground organs present phenotypic variations, but belowground systems can adapt to overcome changes in disturbed areas. Besides, in the process of regeneration of the native community, there are several adjustments that plants perform to grow properly in an area fully exposed to sunlight. In addition, plants from disturbed areas are able to recover the pre-harvest state after one year of aerial biomass removal as plants from natural areas do. Acaulescent palms are greatly distributed in the tropics and they have a diversity of belowground structure forms. Our findings highlight the requirement of further investigations with this large and diverse group of species that present several morphological responses to environmental disturbances. which can contribute to the knowledge of regeneration processes of native palm species from disturbance-prone environments such as the Cerrado.

## 3.3. References

Abrahamson, W. G., Abrahamson, C. R. (2006). Post-fire canopy recovery in two fire-adapted palms, *Serenoa repens* and *Sabal etonia* (Arecaceae). *Florida Scientist*, 69-79.

Abreu, R. C. R., de Assis, G. B., Frison, S., Aguirre, A., Durigan, G. (2011). Can native vegetation recover after slash pine cultivation in the Brazilian Savanna?. *Forest Ecology and Management*, *262*(8), 1452-1459.

Abreu, R. C., Durigan, G., Melo, A. C., Pilon, N. A., Hoffmann, W. A. (2021). Facilitation by isolated trees triggers woody encroachment and a biome shift at the savanna–forest transition. *Journal of Applied Ecology*, *58*(11), 2650-2660.

Abreu, R. C., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. *Science advances*, *3*(8), e1701284.

Antar, G. M., Pivello, V. R., Gerolamo, C. S., Nogueira, A., Sano, P. T. (2022). Herb–subshrub diversity in open savanna sites with distinct fire regimes in the Jalapão region, Brazil. *Journal of Tropical Ecology,* 1-9.

Appezzato-da-Glória, B. (2015). Morfologia de sistemas subterrâneos de plantas. Belo Horizonte, Brazil: 3i editora.

Assis, A. C. C., Coelho, R. M., da Silva Pinheiro, E., Durigan, G. (2011). Water availability determines physiognomic gradient in an area of low-fertility soils under Cerrado vegetation. Plant Ecology, 212(7), 1135-1147.

Barbosa, L. H. S., da Silva, G. S., Júnior, A. F. N., Appezzato-da-Glória, B. (2022). Leaf phenotypic variation of *Allagoptera campestris* (Mart.) Kuntze (Arecaceae) in response to unnatural disturbances in the Cerrado. *Flora*, *287*, 151993.

Bittebiere, A. K., Benot, M. L., Mony, C. (2020). Clonality as a key but overlooked driver of biotic interactions in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *43*, 125510.

Bombo, A. B., Appezzato-da-Glória, B., Fidelis, A. (2022). Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience. *Oecologia*, *199* (1), 153-164.

Bond, W. J. (2022). Out of the shadows: ecology of open ecosystems. *Plant Ecology & Diversity*, *14* (5-6), 205-222.
Callaway, R. M., Pennings, S. C., Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. *Ecology, 84*(5), 1115-1128.

Cássia-Silva, C., Oliveira, R. S., Sales, L. P., Freitas, C. G., Jardim, L., Emilio, T., Bacon, C. D., Collevatti, R. G. (2022). Acaulescence promotes speciation and shapes the distribution patterns of palms in Neotropical seasonally dry habitats. *Ecography*, *2022*(3), e06072.

Chiminazzo, M. A., Bombo, A. B., Charles-Dominique, T., Fidelis, A. (2021). Your best buds are worth protecting: Variation in bud protection in a fire-prone cerrado system. *Functional Ecology*, *35* (11), 2424-2434.

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., Knox, K. J. E. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New phytologist*, *197* (1), 19-35.

Coelho, A. J. P., Magnago, L. F. S., Matos, F. A. R., Mota, N. M., Diniz, É. S., Meira-Neto, J. A. A. (2020). Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. *Biodiversity and Conservation*, *29* (11), 3151-3168.

da Silva, G. S., Ferraro, A., de Aguiar, C. L., Appezzato-da-Glória, B. (2021). Resprouting strategies of three native shrub Cerrado species from a morphoanatomical and chemical perspective. *Australian Journal of Botany*, *69* (8), 527-542.

Dantas, V. D. L., Batalha, M. A., Pausas, J. G. (2013). Fire drives functional thresholds on the savanna–forest transition. *Ecology*, *94* (11), 2454-2463.

Dantas, V. D. L., Hirota, M., Oliveira, R. S., Pausas, J. G. (2016). Disturbance maintains alternative biome states. *Ecology letters*, *19* (1), 12-19.

De Antonio, A. C., Scalon, M. C., Rossatto, D. R. (2020). The role of bud protection and bark density in frost resistance of savanna trees. *Plant Biology*, *22* (1), 55-61.

de Moraes, M. G., de Carvalho, M. A. M., Franco, A. C., Pollock, C. J., Figueiredo-Ribeiro, R. D. C. L. (2016). Fire and drought: soluble carbohydrate storage and survival mechanisms in herbaceous plants from the Cerrado. *BioScience*, *66*(2), 107-117.

DuBois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A.T., Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry,* 28, 350–356.

Endress, B. A., Gorchov, D. L., Noble, R. B. (2004). Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecological applications*, *14*(4), 1139-1153.

Faleiro, R., da Silva, G. S., Pilon, N. A. L., de Aguiar, C. L., Appezzato-da-Glória, B. (2022). Attributes that ensure Cerrado shrub layer resilience after afforestation: The case of *Psidium grandifolium*. *South African Journal of Botany*, *149*, 6-18.

Fernandes, H. (1993). Geographic distribution of palms. In *I International Symposium on Ornamental Palms 360* (pp. 63-70).
Ferraro, A., da Silva, G. S., de Aguiar, C. L., Appezzato-da-Glória, B. (2021). Evaluating belowground bud banks of native species from Cerrado: Structural, chemical, and ecological approaches. *Flora*, *281*, 151852.

Fidelis, A., Appezzato-da-Glória, B., Pillar, V. D., Pfadenhauer, J. (2014). Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands?. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *209*(2), 110-116.

Foster, D. R., Fluet, M., Boose, E. R. (1999). Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological applications, 9* (2), 555-572.

Gerlach, D. (1984). Botanische Mikrotechnik. Georg Thieme Verlag: New York, NY, USA.

Gregow, H., Laaksonen, A., Alper, M. E. (2017). Increasing large scale windstorm damage in Western, Central and Northern European forests, 1951–2010. *Scientific Reports*, *7* (1), 1-7.

Guzmán, B., Fedriani, J. M., Delibes, M., Vargas, P. (2017). The colonization history of the Mediterranean dwarf palm (*Chamaerops humilis* L., Palmae). *Tree Genetics & Genomes*, *13*(1), 1-10.

Herben, T., Šerá, B., Klimešová, J. (2015). Clonal growth and sexual reproduction: tradeoffs and environmental constraints. *Oikos*, *124*(4), 469-476.

Herben, T., Klimešová, J. (2020). Evolution of clonal growth forms in angiosperms. *New Phytologist*, *225*(2), 999-1010.

Higashikawa, E. M., Brasil, M. M. O., Magnusson, W. E. (2019). A 30-year study of the effects of selective logging on a stem-less palm (*Astrocaryum sociale*) in a central-Amazon Forest. *Forest Ecology and Management, 432*, 607-611.

Hoffmann, W. A., Flake, S. W., Abreu, R. C., Pilon, N. A., Rossatto, D. R., Durigan, G. (2019). Rare frost events reinforce tropical savanna–forest boundaries. *Journal of Ecology*, *107*(1), 468-477.

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Göldel, B., Lim, J. Y., Onstein, R. E., Svenning, J. C. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data*, *6* (1), 1-13.

Klimešová, J., Martínková, J., Herben, T. (2018). Horizontal growth: an overlooked dimension in plant trait space. *Perspectives in Plant Ecology, Evolution and Systematics, 32*, 18-21.

Kouassi, K. I., Barot, S., Laossi, K. R., Gignoux, J., Bi, I. A. Z. (2014). Relationships between ramet and genet dynamics in two clonal palms. *Forest ecology and management*, *312*, 101-107.

Ladd, P. G., Crosti, R., Pignatti, S. (2005). Vegetative and seedling regeneration after fire in planted Sardinian pinewood compared with that in other areas of Mediterranean-type climate. *Journal of Biogeography*, *32*(1), 85-98.

Łaska, G. (2001). The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecology*, *157*, 77-99.

Liesenfeld, M. V. A., Vieira, G. (2018). Postfire Palm Resprouting in the Amazonian Forest: are Underground Stems an Advantage?. *Perspectivas Rurales Nueva Época*, *16*(31), 11-23.

Lira-Martins, D., Nascimento, D. L., Abrahão, A., de Britto Costa, P., D'Angioli, A. M., Valézio, E., Rowland, L., Oliveira, R. S. (2022). Soil properties and geomorphic processes influence vegetation composition, structure, and function in the Cerrado Domain. *Plant and Soil*, 1-40.

Loiola, P. P. de., Cianciaruso, M. V., Silva, I. A., Batalha, M. A. (2010). Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *205*(10), 674-681.

Lozano-Parra, J., Pulido, M., Lozano-Fondón, C., Schnabel, S. (2018). How do soil moisture and vegetation covers influence soil temperature in drylands of Mediterranean regions?. *Water*, *10*(12), 1747.

Menezes, L. F. T. D., Araujo, D. S. D. D. (2004). Regeneração e riqueza da formação arbustiva de Palmae em uma consequência pós-fogo na restinga da Marambaia, Rio de Janeiro, RJ, Brasil. *Acta Botanica Brasilica*, *18*, 771-780.

McPherson, K., Williams, K. (1998). Fire resistance of cabbage palms (*Sabal palmetto*) in the southeastern USA. *Forest Ecology and Management*, *109*(1-3), 197-207.

Montúfar, R., Anthelme, F., Pintaud, J. C., Balslev, H. (2011). Disturbance and resilience in tropical American palm populations and communities. *The Botanical Review*, *77* (4), 426-461.

Palmweb (2022). Palmweb: Palms of the World Online. Published on the internet [https://palmweb.org/node/2]. Accessed on [date - 19/08/2022].

Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Glória, B., Fidelis, A. (2018). Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist*, *217*(4), 1435-1448.

Pausas, J. G., Pratt, R. B., Keeley, J. E., Jacobsen, A. L., Ramirez, A. R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I. N., Davis, S. D. (2015). Towards understanding resprouting at the global scale. *New Phytologist*, 209 (3), 945-954.

Pilon, N. A., Durigan, G., Rickenback, J., Pennington, R. T., Dexter, K. G., Hoffmann, W. A., Abreu, R.C.R, Lehmann, C. E. (2021). Shade alters savanna grass layer structure and function along a gradient of canopy cover. *Journal of Vegetation Science*, *32*(1), e12959.

Pinheiro, L. F. S., Pilon, N. A. L., Rossatto, D. R., & Kolb, R. M. (2022). Shade drives plant community changes of ground-layer savanna vegetation: Short-term changes under an experimental approach. *Journal of Vegetation Science*, *33*(2), e13118.

Phillips, A. J., Leger, E. A. (2015). Plastic responses of native plant root systems to the presence of an invasive annual grass. *American Journal of Botany*, *102*(1), 73-84.

Poorter, L., Kitajima, K., Mercado, P., Chubiña, J., Melgar, I., & Prins, H. H. (2010). Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology, 91* (9), 2613-2627.

Quattrocchi, U. (2018). CRC World Dictionary of Palms: Common Names, Scientific Names, Eponyms, Synonyms, and Etymology Volume I Arecaceae A–G. CRC Press.

Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N., Ulloa Ulloa, C. (2020). The distribution of biodiversity richness in the tropics. *Science Advances*, *6*(37), eabc6228.

Reynolds, H. L., D'antonio, C. (1996). The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant and soil*, *185*(1), 75-97.

Rosenberg, M.S., Rothstein, H.R., Gurevitch, J. (2013). *Effect Sizes: Conventional Choices and Calculations*. *Handbook of meta-analysis in ecology and evolution* (ed. by J. Koricheva) and J. Gurevitch), pp. 61–71. Princeton University Press, New Jersey.

Rossatto, D. R., de Araújo, P. E., da Silva, B. H. P., Franco, A. C. (2018). Photosynthetic responses of understory savanna plants: Implications for plant persistence in savannas under tree encroachment. *Flora, 240*, 34-39.

Silva, G. S., Ferraro, A., Ogando, F. I., Aguiar, C. L., Appezzato-da-Gloria, B. (2020). Structures related to resprouting potential of two Myrtaceae species from Cerrado: morpho-anatomical and chemical studies. *Anais da Academia Brasileira de Ciências*, *92*.

Strasburger, E. (1913). Handbook of practical botany. George Allen & Company Ltda: London, UK.

Svenning, J. C. (2000). Growth strategies of clonal palms (Arecaceae) in a neotropical rainforest, Yasuni, Ecuador. *Australian Journal of Botany*, *48*(2), 167-178.

Tribble, C. M., Martínez-Gómez, J., Howard, C. C., Males, J., Sosa, V., Sessa, E. B., Cellinese, N., Specht, C. D. (2021). Get the shovel: morphological and evolutionary complexities of belowground organs in geophytes. *American Journal of Botany, 108*(3), 372-387.

Valladares, F., Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 237-257.

Vesk, P. A., Westoby, M. (2004). Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology*, 310-320.

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, *36*, 1–48.
Zanzarini, V., Zanchetta, D., Fidelis, A. (2019). Do we need intervention after pine tree removal? The use of different management techniques to enhance Cerrado natural regeneration. *Perspectives in ecology and conservation*, *17* (3), 146-150.

Zeppel, M.J.B., Harrison, S.P., Adams, H. D., Kelley, D.I., Guangqi, L., Tissue, D.T., Dawson, T.E., Fensham, R., Medlyn, B.E., Palmer, A., West, A.G., McDowell, N.G. 2015. Drought and resprouting plants. *New Phytologist*. 206, 583–589.

Zupo, T., Daibes, L. F., Pausas, J. G., Fidelis, A. (2021). Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science, 32* (1), e12968.