ными связями молекулы лигнина между собой и простыми эфирными связями его макромолекулы с полисахаридами, боковые цепочки которых состоят из остатков арабинозы, ксилозы и глюкозы. Количество углеводов и состав оксикоричных кислот меняется в ходе лигнификации.

Согласно данным гель-хроматографии, лигнин, синтезированный на первых стадиях процесса, из-за связей с полисахаридами клеточной стенки имеет повышенную молекулярную массу и более однороден, чем на последующих стадиях формирования трахеид. В ходе биосинтеза средняя молекулярная масса препаратов лигнина меняется, и дисперсность полимера возрастает. Дисперсность лигнина, выделенного из зрелой поздней ксилемы, выше, чем ранней. Он содержит фракции с высокой молекулярной массой. Возможно, часть высокомолекулярного лигнина локализована в срединной пластинке. ИК-спектры показали различие в структуре полимера ранних стадий лигнификации двух типов ксилемы с одной стороны, с другой – усиление конденсации фенилпропановых единиц по мере созревания трахеид. Данные указывают на последовательные изменения в структуре лигнина в ходе лигнификации ранней и поздней ксилемы, приводящие к гетерогенности полимера зрелой ксилемы годичных приростов в хвойных.

THE MORPHOLOGY AND FUNCTION OF UNDERGROUND SYSTEMS OF SPECIES FROM BRAZILIAN SAVANNA

Appezzato-da-Glória B.[1]; Soares A. N.[1]; Silva J. M.[1]; Bombo A. B.[1]; Martins A. R.[2]; Fidelis A.[3]

[1]Department of Biological Sciences, Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo,13418-900, Piracicaba, SP, Brazil; anielcasoares@hotmail.com; aline_bbombo@hotmail.com; bagloria@esalq.usp.br
[2]Institute of Biology, Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brazil;
[3]Department of Ecology, Universidade de São Paulo, 05508-900, São Paulo, Brazil;

The Brazilian Cerrado, a neotropical savanna, covers approximately 2 million km2, representing about 23 % of the area of the country. This vegetation presents a wide physiognomic variation (Fig. 1): *campo limpo*, a grassland, to *cerradão*, a tall woodland. The intermediate physiognomies (*campo sujo* a shrub savanna, *campo cerrado* a savanna woodland, and *cerrado sensu stricto* a woodland) are considered ecotones of the two extremes. There are different physiognomies due to distinct factors, such as deep and well drained soils that are acidic and with high aluminum content, seasonality, with dry periods of 3–4 months, and fire [6].

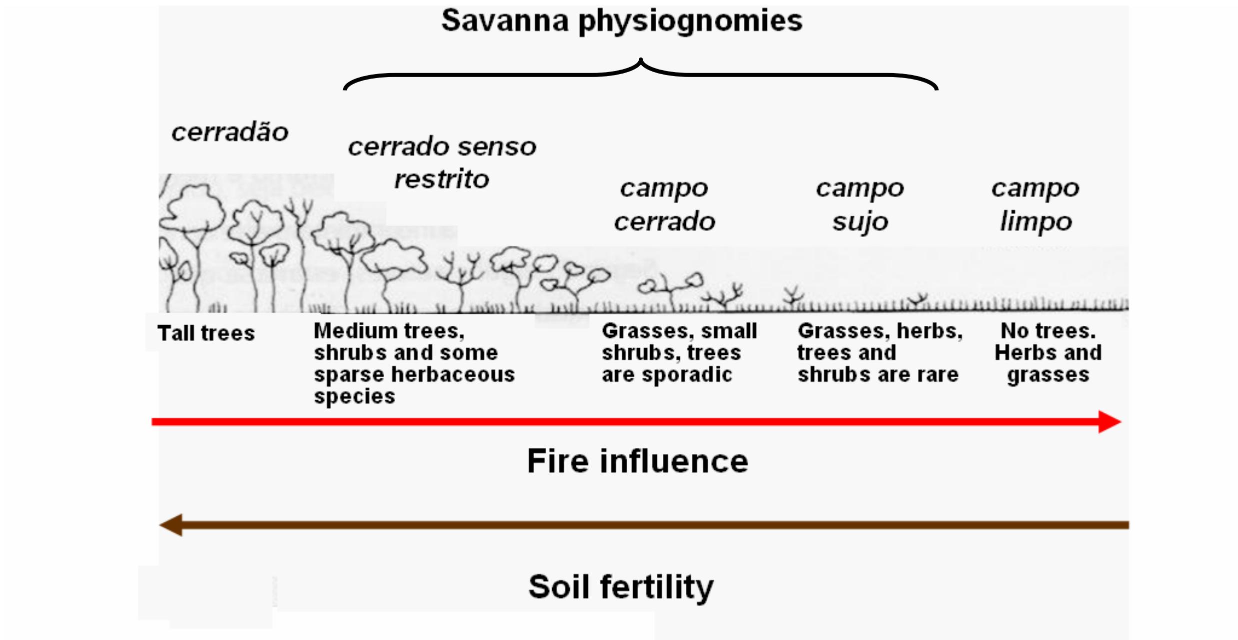


Figure 1. Influence of the fire and soil fertility in the Brazilian Cerrado physiognomies (based on Coutinho [6])

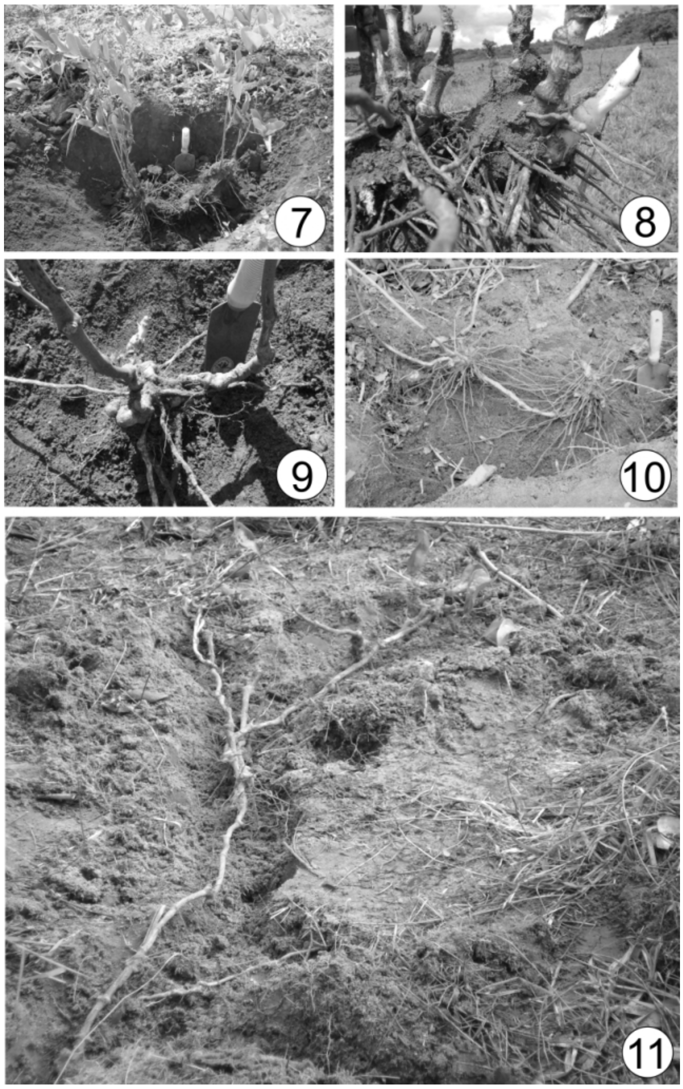
The Cerrado flora presents two main components: the herbaceous and the woody, which are floristically distinct and antagonistic, because both are sun-loving. Species from the herbaceous and subshrub strata are dominant in open physiognomies («campos», grasslands). As a result of seasonal climate with dry periods of three to four months, usually associated with the action of fire, the vegetation of the Cerrado has several mechanisms that include morphological and physiological adaptations that allow plants to survive adverse conditions. Among the morphological adaptations of the herbaceous and subshrubby species we highlight the thickened underground systems. Regarding phenology, several species exhibit seasonal growth of this stratum, i.e., in the autumn shoots wither and die persisting only thickened underground systems [8]. During spring and the beginning of rainy season, individuals rapidly resprout and flower using the reserves stored in the underground structures. Asteraceae is the most represented family in the Cerrado after the Fabaceae, that is, it is the second one with the most number of species [14]. Almeida *et al.* [1] studied eight Cerrado fragments in the State of São Paulo (Brazil) from 2000 to 2002 to produce an inventory of Asteraceae species. Their species list was then compared to other 24 Cerrado species lists in the literature. According to these authors amongst the most frequent species are *Chresta sphaerocephala, Chromolaena squalida*, *Lessingianthus bardanoides, Orthopappus angustifolius* and *Piptocarpha rotundifolia.* It is possible that this higher frequency is related to the presence of belowground buds in the Cerrado as demonstrated in species of North American praires [5]. But in the Cerrado there are types of underground systems other than rhizomes that are usually described in the praire. The terminology of these belowground structures is also different and it is presented here. The first scientific study carried out on the vegetation of the Brazilian Cerrado, where different underground organs were illustrated was "Lagoa Santa", published in 1892 by Eugen Warming [20]. In the 40's stand out studies of Felix Rawitscher, Mercedes Rachid and Mario Guimarães Ferri on vegetation in the savanna of São Paulo State, Brazil. The authors divided the vegetation according to the strategy of exploitation of soil water by roots: **a)** shrubs and small trees with very deep roots, many of which vegetate during the entire dry season; **b)** grass with shallow roots, they shrivel when the water drained and, **c)** plants that vegetate only during the rainy season, many of which have bud-bearing underground organs able to retain high percentage of water [16]. Regarding the effect of fire in open areas of the Cerrado, Rachid [16] observed that **xylopodium**, term introduced by Lindman in 1900 for a lignified underground system very common in grasslands of southern part of Brazil [12], and tuberous roots survive to fire, although it can be seen charred branches on the soil surface. In fact, Coutinho [6] shows that after the fire the soil surface temperature is about 74°C so that, the temperature drops dramatically at 1, 2, 3 and 5 cm deep. At 1 cm deep not exceeding 55°C and at 5 cm showing an increase of only a few degrees. So the fire burns the shoots, but the underground system keeps alive.

Figure 2. Underground system of Mandevilla illustris (Apocynaceae). It is constituted by a xylopodium (upper slender portion) and a tuberous root. Bar = 6cm.

Inn the 60's, Carlos Rizzini and Heringer Ezechias [17,18,19] studying savanna species show the distinction between the tuberous roots and xylopodium and new terminology such as **secondary xylopodium, 'initial tubercles' on trees and diffuse underground system** [19]. Xylopodium is a perennial thickened woody organ with numerous buds situated superficially, in the driest soil part, therefore it is almost always associated with tuberous roots that provide it with water and food reserves in order to survive the dry season and, later on, resprout as verified in *Mandevilla illustris* (Fig. 2). Secondary xylopodium is formed on some tree and shrub species, for example, in *Stryphnodendron barbatiman*, *Palicourea rigida* and *Kielmeyera coriacea* (a Fabaceae, Rubiaceae and Clusiaceae respectively) in response to elimination of aerial stems caused by fire (Fig. 3). It is a thickening at the stem base capable of resprouting in the rainy season. The 'initial tubercles' are found, for example, in *Annona crassiflora*, *Piptadenia macrocarpa* and *Tabebuia caraiba* (a Annonaceae, Fabaceae and Bignoniaceae respectively). They are thickened roots in the early stages of plant development in order to accumulate reserves and water. As development proceeds the thickenings are no longer perceived as the tap root becomes axial and deep. Interestingly, several species of herbaceous and shrub species in the savanna formations thicken the primary root soon after germination, as in *Mandevilla illustris* and *M. velutina* [14] which allows the rapid establishment in the field. Many Cerrado species, as *Chresta sphaerocephala*, show an unusual behavior. A single individual plant can occupy an area of about 10 m in diameter [1]. They have a complex profusely branched and superficial subterranean system described by Rizzini and Heringer [19] as 'diffuse underground systems' (Fig. 4-6). Some of these diffuse underground systems are caulinar structures named 'soboles' as verified in *Erythroxylum nanum* [8] or radicular structures named 'gemmiferous roots' as described in *Chresta sphaerocephala* [1]. They have vegetative reproduction sprouting in different directions, but all the shoots are interconnected belowground, forming an extensive, complex system. Colonies of *Annona pygmaea, Andira humilis, Pradosia brevipes, Parinari obtusifolia,* among others, can reach several meters in diameter [20]. A similar pattern can be seen for *Chresta sphaerocephala,* where the aerial stems can be as far as 100 cm apart and shows diffuse underground systems [8].

Figures 3–6. 3. A common view in Cerrado, carbonized base of some branches emitted in previous periods. 4–6. Diffuse underground systems. *Hymenaea stigonocarpa* (4), *Kielmeyera variabilis* (5, 6).

According to Filgueiras [8] this phenomenon seems to be quite widespread and should be investigated in depth due to difficulties found to define an individual in Cerrado vegetation types, being of crucial importance for population biology and community studies. These systems were consequences of repeated destruction of the aerial biomass, due to fire disturbance, affecting thus, the reproduction by seeds and stimulating shoot bud-forming roots [8]. The remaining carbonized base of some branches emitted in previous periods from the diffuse underground system of *Chresta sphaerocephala* confirms the interference of the fire in the sprouting process [2]. Another type of underground system found in the Cerrado is **rhizophore** [15].Rhizophores constitute the underground cauline system in plants which have bipolar cauline ramification system, that is, both aerial (plumule origin) and underground systems (cotyledonary buds origin). Underground cauline systems play an important role increasing the plant rhizosphere, as well as functioning for storage and resprouting [15, 10]. *Smilax* rhizophores distribution (0–20cm soil depth) in *S. brasiliensis* (Fig. 7, 8), *S. campestris*, *S. cissoides*, *S. goyazana*, *S. oblongifolia* (Fig. 9) [13], *S. polyantha* (Fig. 10) and *S. fluminensis*(Fig. 11) coincides with higher contents of organic matter whether the soil being stony or not. All of them exhibited clonal growth hence their underground system functions as storage structures and the axillary buds can sprout into new stems. Only *Smilax fluminensis*, collected in sandy soil of *campos cerrados*, presents vegetative dispersal due to the runners (Fig. 11).



Figures 7-11. Smilax rhizophores distribution in S. brasiliensis (7, 8), S. oblongifolia (9), S. polyantha (10) and S. fluminensis(11)

Therefore bud-bearing underground systems could contribute to the formation of a belowground bud bank in the Cerrado [4]. Bud bank was first described in 1977 by Harper [9] and its concept was expanded by Klimesova and Klimes [11]. It comprises all buds from plants, which can be potentially used for vegetative regeneration by the formation of new shoots after the partial or total removal of aboveground parts caused by extreme climatic factors as drought or fire. Recently, the importance of underground systems of the bud bank for the regeneration of vegetation after disturbance and on the maintenance of plant populations were described for the subtropical grasslands in Southern Brazil [7]. Studies have shown that these grasslands are resilient to fire, with a great capacity for regeneration after disturbance [16]. Most of the vegetation regrowth, mainly from buds protected below ground level, found in underground organs such as rhizomes and xylopodium. Thus, the successful regeneration of the vegetation depends on the survival of these organs, as well as the viability of buds [16]. The same strategy might be found in Cerrado, since vegetation experiences frequent fires and a great part of the herbaceous and shrub strata show species with the presence of bud-bearing belowground organs. However, there are no studies about the bud banks of Cerrado vegetation.

LITERATURE

1. *Almeida, A. M., C. R. Fonseca, P. I. Prado, M. Almeida-Neto, S. Diniz, U. Kubota, M. R. Braun, R. L. G. Raimundo, L. A. Anjos, T. G. Mendonça, S. M. Futada, T. M.* Lewinsohn. Diversidade e ocorrência de Asteraceae em cerrados de São Paulo // Biota Neotropica. 2005. 5. P. 1–17.
2. *Alonso, A. A., Machado, S.R.* Morphological and developmental investigations of the underground system of Erythroxylum species from Brazilian cerrado // Australian Journal of Botany. 2007. 55. P. 749–758.
3. *Appezzato-da-Glória, B., Estelita, M.E.M.* The developmental anatomy of the subterranean system in Mandevilla illustris (Vell.) Woodson and M. velutina (Mart. ex Stadelm.) Woodson (Apocynaceae) // Revista Brasileira de Botânica. 2000.23/ P. 27–35.
4. *Appezzato-da-Gloria, B.; Cury, G.; Soares, M. K. M.; Hayashi, A. H.; Rocha, R.*. Underground systems of Asteraceae species from the Brazilian Cerrado // Journal of the Torrey Botanical Society. 2008. 135(1). P. 103–113.
5. *Benson, E. J., D. C. Hartnett, K. H. Mann*. Belowground bud banks and meristem limitation in tallgrass prairie plant populations // Am. J. Bot. 2004. 91. P. 416–421.
6. *Coutinho, L. M*. Fire in the Ecology of the Brazilian Cerrado // Fire in the tropical biota. Springer-Verlag, Berlim, DE. 1990. P. 82–105,
7. *Fidelis, A., Appezzato-da-Glória, B. and Pfadenhauer, J.* A importância da biomassa e estruturas subterrâneas nos Campos Sulinos In: Pillar, V.D.; Müller, S.C.; Castilhos, Z.M.S.; Jacques, A.V.A. [Org.]. Os Campos Sulinos: conservação e uso sustentável da biodiversidade. Brasília: Ministério do Meio Ambiente, Brazil. 2009.
8. *Filgueiras, T. S.* Herbaceous Plant Communities // The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York, NY. 2002. P. 121–139,
9. *Harper J.L.* Population biology of plants. Academic Press, New York. 1977.
10. *Hayashi, A.H., Appezzato-da-Glória, B.* The origin and anatomy of rhizophores in Vernonia herbacea and V. platensis (Asteraceae) from Brazilian Cerrado // Australian Journal of Botany. 2005.53(3). P. 273–279.
11. *Klimešová, J., L. Klimeš.* Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessment. Perspect // Plant Ecol. Evol. Syst. 2007. 8: 115–129.
12. *Lindman, C. A. M.* Vegetationen i Rio Grande do Sul (Sydbrasilien). Nordin & Josephson, Stockholm. 1900. 239 p.
13. *Martins, A. R., Pütz, N.; Soares, A. N.; Bombo, A. B.; Appezzato-da-Gloria, B*. New approaches to underground systems in Brazilian Smilax species (Smilacaceae) // Journal of the Torrey Botanical Society. 2010.137 (2–3). P. 220–235.
14. *Mendonça, R. C., J. M. Felfili, B. M. T. Walter, M. C. Silva Júnior, A. V. Rezende, T. S. Filgueiras, P. E.* Nogueira. Flora vascular do Cerrado // Cerrado: ambiente e flora. EMBRAPA-CPAC Planaltina, GO. 1998. P. 289–257
15. *Menezes NL, Müller C, Sajo MG* Um novo e peculiar tipo de sistema subterrâneo em espécies de Vernonia da Serra do Cipó (Minas Gerais, Brasil) // Boletim de Botânica da Universidade de São Paulo.1979. 7. P. 33–38.
16. *Rachid, M.* Transpiração e sistemas subterrâneos da vegetação de verão dos campos cerrados de Emas // Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo. 1947. 80. P. 1–140.
17. *Rizzini, C.T., Heringer, E.P.* Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium // Phyton. 1961. 17. P. 105–124.
18. *Rizzini, C. T., E. P. Heringer.* Studies on the underground organs of trees and shrubs from some southern Brazilian savannas // An. Acad. Bras. Cienc. 1962. 34. P.235–247.
19. *Rizzini, C. T., E. P. Heringer*. Estudo sobre os sistemas subterrâneos difusos de plantas campestres // An. Acad. Bras. Cienc. 1966. 38. P. 85–112.
20. *Warming, E*. Lagoa Santa. (Trad. De A. Loefgren), Belo Horizonte.1908.