

ALLELOPATHY AND FIRE CYCLE IN BRAZILIAN CERRADO

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ABSTRACT: Allelopathy refers to the effect of biochemical interactions from one plant to another plant including inhibitory and stimulatory effects. The products, allelochemicals are highly toxic, and the production of these compounds not only can be stimulated by plants and microorganism, but also by environment factors e.g. water stress, nutrient deficiency and temperature where these conditions are commonly found in the cerrado environment. Cerrado region is rich of plants which produce secondary metabolite, especially phenolic compounds and numerous vegetations have been investigated of their inhibitory effects on other crops developments. It is known that allelopathy is a key process regulating plant regeneration in many world ecosystems including savanna/cerrado. The interest of allelopathic study in shrub ecosystems rises as a result of inadequate natural regeneration and reduced growth of planted seedlings that has been attributed to the release of allelochemicals by herbaceous vegetation. Fires, whether they are natural or human made, are a common characteristic of this biome and its presence is considered to be an important ecological factor and responsible for regulating species diversity. Following fire, the negative effects of allelochemicals are removed or reduced. However, numerous ecological factors of cerrado have been associated with seedling survival, not only caused by plant toxin, but also low soil fertility, low water, temperatures and animal predation. This paper reviews the presence of cerrado vegetation that launched toxic compounds and their allelopathic effects on other plants, the presence of savanna fire and post-fire ecological impacts. In general, the main objective of this paper is to point out the allelopathy and fire-related impacts to provide us to solve ecological issues concerning to the sustainable development of the cerrado.

Keywords: Allelopathy. Cerrado. Fire cycle. Post-Fire impacts.

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INTRODUCTION

Allelopathy reveals how plants use secondary metabolite products to stress the neighboring plants. The products are called allelochemicals that can be present in roots, leaves, seeds, flowers, rhizomes, stems and pollen of plants and the delivery of chemical effect into plant receiver is often occurs through root exudation, volatilisation, leaching or decomposition of residues (Inderjit & Dakshini, 1994). Rice (1984) classified allelochemicals produced by higher plants and microorganism into numerous categories: water soluble organic acid, straight chain alcohols, aliphatic aldehydes and ketones; simple unsaturated lactones; long-chain fatty acids and polyacetylenes; phenolic, benzoic acid and its derivatives; cinnamic acid and its derivatives; quinines (benzoquinone, anthraquinone and complex quinines); flavonoids; tannins; terpenoids and stereoids, amino acids; alkaloids and cyanohydrins; sulfuret; purines and nucleotides. The biosynthetic pathways of allelopathic substances are shown in **Fig. 1**.

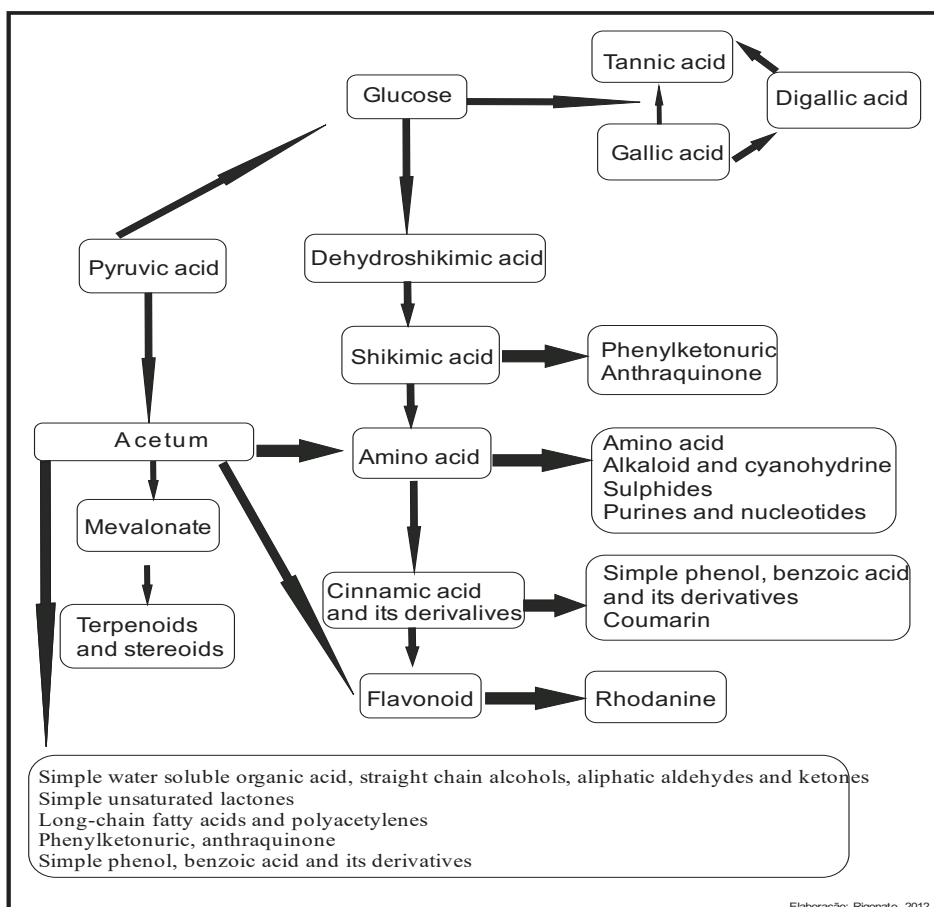


Figure 1 – The biosynthetic pathways of allelopathic substances Source: Li et al., (2010)

These secondary metabolites in plants have been investigated by phytochemists and classified as waste products and play an important role in shaping interactions and communities (Li et al. 2010). In agro ecosystem, these compounds have harmful effects on the growth of associated and next-season crops (Rice, 1984) and in forest ecosystem allelochemicals can inhibit the growth of competing vegetation (Ridenour & Callaway, 2001). The action of allelochemicals can be divided into indirect and direct action. Indirect action may include the effect on alteration of soil property, its nutrition and an altered population and activity of harmful or beneficial organism like microorganism (Rizvi et al., 1992) while direct action includes the effects of allelochemicals on various aspects of plant growth and metabolism. Rice (1984) stated that in most cases, these compounds inhibit at higher concentration and stimulate at smaller ones. The main locations and processes known to be attacked by allelochemicals are cytology and ultrastructure, phytohormones and their balance, membrane and its permeability, germination of pollens/spores, respiration, protein synthesis, pigment synthesis and photosynthesis, nitrogen fixation and enzyme activity.

A classic example of allelopathy is the allelochemical of Black walnut tree (*Juglans nigra*). The tree produces the allelochemical juglone (5-OH-1,4-naphthoquinone), when exposed to the air or soil components, this compound is immediately transformed into the oxidized and highly toxic form (Thakur & Cahalan, 2011). Crist and Sherf (1973) confirmed the numbers of plants walnut sensitive are tomato, potato, pea, apple, cucumber, watermelon, bean, garden cress, corn and many ornamental ericaceous species such as *rhododendron* and *azalea*. The physiology and mechanism of the action of Juglone also have been done and demonstrated that the allelochemical Juglone inhibits plant growth by reducing leaf photosynthesis, transpiration, stomatal conductance and leaf/root respiration in soybean and corn (Jose & Gillespie, 1998). The chemical also known as an inducer of oxidative stress on growth and development of maize seedlings (Sytykiewicz, 2011), reduced chlorophyll a,b content and decreased some anatomical structures such as stomata and xylem vessel on growth cucumber seedling (Terzi et al., 2003).

Brazilian cerrado is considered to be a biome extremely complex that provides a great potential for the use of its biodiversity. The cerrado is a vast tropical savanna region of Brazil that represents approximately 23% of the country land (± 2 million km²). According to Sano et al. (2008), the cerrado occupy portion central of Brazil including states of Bahia, Goiás, Mato Grosso do Sul, Mato Grosso, Maranhão, Minas Gerais, Paraná, São Paulo, Tocantins and District Federal. Mendonça et al. (2008) listed the total vascular flora of the cerrado were 12,356 species and represented between 20 – 50% of the total of the Brazilian species. The herbaceous sub-shrub species in this region represents 57% whereas 43% was the endemic plants (Mendonça et al., 2008; Klink & Machado, 2005).

The cerrado soil is acid, nutrient-poor and high content of aluminum. The climate is hot and semi humid with rain season (October – April) and dry season (May – September). There is a great variation of trees and herbaceous vegetation in the cerrado formation: grassland savanna, savanna and seasonal forest (Ribeiro et al., 1983). During dry season, the lands are exposed to fire either by a natural fire or by human-made. In the last decades, the fire frequency has been increased due to the increase of agriculture and pasture. Along with seasonal rains and less nutrients in the soil, the fire has given an importance ecological impact in determining the structure of the vegetations (Moreira, 2000).

According to Einhelling (1996), a production of allelochemicals can be stimulated either by plants and microorganism or by environment factors e.g. water stress, nutrient deficiency and temperature commonly found in the cerrado nature (Oliveira et al., 2004a). In ecosystems with a high frequency of fires, allelochemicals can indeed be a consequence of physical damage caused by fire or a strategy to reduce the proliferation of large quantities of fuelwood near the donor plant. Allelochemicals are chemical compounds produced by plants that can influence the growth and development of other organisms in their environment, including neighboring plants. Following a fire, plants may suffer physical damage such as leaf scorching or even complete burning. This physical damage can trigger the release of allelochemicals as a defense response. The allelochemicals released by the damaged plants can have various effects on other plants in the ecosystem. They may inhibit the germination or

growth of nearby plants, acting as a form of chemical competition. This can help reduce the competition for resources such as sunlight, water, and nutrients, allowing the damaged plant to recover and regrow more efficiently after the fire. Additionally, in fire-prone ecosystems, the presence of large quantities of fuelwood near the donor plant can pose a significant risk. Fuelwood refers to dead plant material, such as fallen branches, twigs, and leaves, that can fuel the spread of fire. By producing allelochemicals, the donor plant can potentially reduce the accumulation of fuelwood in its immediate vicinity. The allelochemicals released by the plant may inhibit the growth or decomposition of dead plant material, slowing down the accumulation of fuelwood and reducing the risk of intense fires in the area. Therefore, allelochemicals in ecosystems with high fire frequency can be a consequence of physical damage caused by fire and serve as a strategy to reduce the proliferation of large quantities of fuelwood near the donor plant. These chemical compounds play a role in plant defense, competition, and fire management in fire-prone ecosystems. (Williamson et al., 1992). Mallik (2003) affirmed that fire is an important factor in reducing the concentration of allelochemicals in forest soils, burning through the humus and litter high concentrations of growth inhibitors. The main objective of this paper is to discuss the allelopathic and its fire-related impacts in cerrado community in order to provide us to solve ecological issues concerning to the sustainable development of the region.

ALLELOPATHIC ACTIVITIES IN BRAZILIAN CERRADO ECOSYSTEMS

Allelopathy is a key process regulating plant regeneration in many world ecosystems. In forest ecosystems, allelochemicals produced by invasive plants can inhibit the growth of competing vegetation, thereby providing the invader with a competitive advantage (Li et al., 2010). The interest of allelopathic study in forest ecosystems rises as a result of inadequate natural regeneration and reduced growth of planted seedlings that has been attributed to the release of allelochemicals by herbaceous vegetation (Kruse, 2000). For instance, phenolic allelochemicals of ericaceous plants have been associated to the regeneration failure of conifers in boreal and temperate forests (Mallik, 2003). By forming protein-phenol complexes, the allelochemicals cause a further reduction of available nitrogen causing a soil nutrient

imbalance. In Brazilian cerrado ecosystems, many studies of allelopathy have focused on invasive species and plants for agriculture interest or on identifying and isolating chemical substances with potential use as herbicides. A number of plants have been investigated more or less thoroughly for allelopathic activity towards cultivated plants (Table 1).

Table 1. Allelopathic potential of various plants species in cerrado ecosystem

Species	Family	Fraction of plants extract /leachates	Allelopathic effect	References
Shrubs				
<i>Andira humilis</i> Mart.	Fabaceae	leaf, stem	germination and growth of <i>Lactuca sativa</i> L., <i>Raphanus sativus</i> L. and <i>Sesamum indicum</i> L.	Periotto et al. (2004); Menezes et al. (2008)
<i>Aristolochia esperanzae</i> O. Kuntze	Aristolochiaceae	leaf, root	seedling growth of <i>Raphanus sativus</i> L., <i>Sesamum indicum</i> L. and <i>Triticum aestivum</i> L.	Gatti et al. (2004, 2010); Jatoba (2010)
<i>Campomanesia adamantium</i> Camb.	Myrtaceae	leaf	root growth of <i>Sesamum indicum</i> L.	Borghetti et al. (2005)
<i>Davilla elliptica</i> St. Hil.	Dilleniaceae	leaf	germination of <i>Lactuca sativa</i> L.	Gatti (2008)
<i>Diospyros hispida</i> A.D.	Ebenaceae	leaf	germination of <i>Lactuca sativa</i> L., <i>Sesamum indicum</i> L. (strong inhibition on dry season)	Gatti (2008)
<i>Miconia albicans</i> (Sw.) Triana	Melastomataceae	leaf	germination and root growth of <i>Cucumis sativus</i> L, <i>Lycopersicum esculentum</i> Mill., <i>Lactuca sativa</i> L., <i>Sesamum indicum</i> L.	Gorla and Perez (1997); Gatti (2008)
<i>Schefflera vinosa</i> (Cham. & Schltdl.) Frodin	Araliaceae	leaf	germination of <i>Lactuca sativa</i> L., <i>Sesamum indicum</i> L.	Gatti (2008)
<i>Solanum lycocarpum</i> St. Hil.	Solanaceae	seed leaf, fruit	germination of <i>Cosmos sulphureus</i> Cav. germination, shoot/root growth of <i>Sesamum indicum</i> L., protein synthesis of <i>Sesamum indicum</i> L.	Borghetti, Pessoa (1997); Oliveira et al. (2004ab); Aires et al. (2005); Jeronimo et al. (2005)
<i>Trembleya parviflora</i> (D.Don) Cogn	Melastomataceae	leaf	root development of <i>Sesamum indicum</i> L.	Borghetti et al. (2005)
Herbaceous				
<i>Brachiaria decumbens</i> Stapf.	Poaceae	leaf	initial growth of <i>Glycine max</i> L., <i>Lactuca sativa</i> L., <i>Zea mays</i> L., <i>Euphorbia heterophylla</i> L. and grass	Maciel et al. (2003); Ramos & Valente

		shoot, root	(<i>Phalaris canariensis</i> L., <i>Melinis minutiflora</i> P. Beauv.) germination of <i>Cajanus cajan</i> L. Millsp.	(1997); Barbosa (2008) Fagioli et al. (1997)
<i>Pennisetum americanum</i> (L.) Leeke]	Poaceae	leaf	germination, mycorrhizal colonization and initial growth of <i>Zea mays</i> L., <i>Glycine max</i> L. and <i>Phaseolus vulgaris</i> L.	Faria et al. (2009)
<i>Pyrostegia venusta</i> (Ker Gawl.) Miers	Bignoniaceae	leaf	main root length and number of secondary root of <i>Cucumis sativus</i> L.	Silva et al. (2011)
<i>Stizolobium aterrimum</i> Piper & Tracy	Fabaceae	leaf	germination, mycorrhizal colonization and initial growth of <i>Zea mays</i> L., <i>Glycine max</i> L. and <i>Phaseolus vulgaris</i> L.	Faria et al. (2009)
Trees				
<i>Anadenthera macrocarpa</i> (Benth.)	Fabaceae	leaf	germination of <i>Brassica chinensis</i> L., <i>Lactuca sativa</i> L.	Silva et al. (2010)
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	leaf	germination of <i>Brassica chinensis</i> L. and <i>Lactuca sativa</i> L.	Silva et al. (2010)
<i>Caryocar brasiliensis</i> Camb.	Caryocaraceae	leaf	germination and initial growth of <i>Biden pilosa</i> L., weed (<i>Digitaria horizontalis</i> Willd., <i>Melinis minutiflora</i> P. Beauv.), <i>Panicum maximum</i> Jacq. vr. and <i>Zea mays</i> L.	Aires (2007); Moreira et al. (2009)
<i>Copaifera langsdorffii</i> Desf.	Fabaceae	leaf, stem, soil below the canopy	germination and root development of <i>Lactuca sativa</i> L.	Santana (2006); Silva et al. (2012)
<i>Eugenia dysenterica</i> Mart. Ex. DC.	Myrtaceae	leaf	germination and initial growth of <i>Biden pilosa</i> L., weed (<i>Digitaria horizontalis</i> Willd., <i>Melinis minutiflora</i> P. Beauv.), and culture crops (<i>Zea mays</i> L., <i>Sesamum indicum</i> L.)	Aires (2007); Gatti et al. (2005)
<i>Kielmeyera coriacea</i> Mart.	Cluciaceae	leaf	germination of <i>Lactuca sativa</i> L., <i>Sesamum indicum</i> L.	Gatti (2008)
<i>Magonia pubescens</i> St. Hil.	Sapindaceae	seed layer	germination and initial growth of <i>Cucumis</i>	Alves & Teixeira (2012)

			<i>sativus</i> L.	
<i>Ouratea spectabilis</i> (mart.) Engl.	Ochnaceae	leaf	germination of <i>Latuca sativa</i> L.	Silva et al. (2006)
<i>Piptocarpha rotundifolia</i> (Less.) Baker	Asteraceae	leaf	germination of <i>Lactuca sativa</i> L., <i>Sesamum indicum</i> L.	Gatti (2008)
<i>Pouteria ramiflora</i> (Mart.) Radlk.	Sapotaceae	leaf	germination of <i>Latuca sativa</i> L.	Silva et al. (2006)
<i>Qualea grandiflora</i> Mart.	Vochysiaceae	leaf	germination of <i>Latuca sativa</i> L.	Felippe (1990); Silva et al. (2006)
<i>Qualea parviflora</i> Mart.	Vochysiaceae	leaf	germination and initial growth of <i>Biden pilosa</i> L., weed (<i>Digitaria horizontalis</i> Willd., <i>Melinis minutiflora</i> P. Beauv.) and <i>Zea mays</i> L.	Aires (2007)
<i>Stryphnodendron adstringens</i> (Mart.) Coville	Fabaceae	leaf	germination and development of <i>Latuca sativa</i> , <i>Cucumis sativus</i> L, <i>Lycopersicum esculentum</i> Mill.	Barreiro et al. (2005); Silva et al. (2006); Manoel et al. (2009)

1. Allelopathic effects studied

The Fabaceae, so far, are the plants family most studied including cerrado shrubs, herbaceous and trees. *Stryphnodendron adstringens* (Mart.) Coville is a cerrado trees that are widely distributed in state of Pará and Mato Grosso do Sul (Barreiro et al., 2005). Allelochemicals agents present on the tree are tannins, alkaloids, flavonoids, (Simões et al., 1999) where the bark has a tendency for higher production of tannins in the warm and wet season (Santos et al., (2006). Other Fabaceae, *Brachiaria decumbens* Stapf. have a great competitive ability over cerrado herbaceous species and are considered the most threatening invasive plants in the community (Zaidan e Carreira, 2008). This fact brought up to study the possibility of the plants to have allelopathic effects (Maciel et al., 2003; Ramos & Valente, 1997; Barbosa, 2008; Fagioli et al., 1997). One of shrub species studied is *Aristolochia esperanzae* O. Kuntze that produced allelochemicals terpenoides, lignoides, alkaloid and phenol derivatives (Lopes & Bolzani, 1988). The leaf and root extracts demonstrated a significant reduction in the size of root xylem cells and in the primary root of *Sesamum indicum* (Gatti et al., 2010), *Lactuca sativa* (lettuce), *Raphanus sativus* (radish) seedlings (Gatti et al., 2004) and on the initial growth of *Triticum aestivum* L. Jatoba (2012). The majority reported results are inhibition effect on seed germination, effects on

coleoptile elongation and on radicle, shoot and root growth. Few studies have been directed to the effects on plants physiologies and structures such as the effect of alkaloid and phenol derivative of *Solanum lycocarpum* St. Hil., a common native shrub in cerrado on protein synthesis (Jeronimo et al., 2005). It may be due to the complexity of allelopathic interaction based on plant physiology whereas seedlings growth is generally considered to be the most susceptible stages. The authors demonstrated the allelochemical effect on the changes in protein turnover. Protein homogenates were prepared from root and shoot parts after 48 hours of incubation both in water and in the extract at 1%. Six hours before protein extraction ³⁵S-methionine (about 30 μ Ci/seedling) was applied on the root hairs. The proteins were dissolved in a modified Laemmli buffer (Tris 80mM, SDS 2%, β -mercaptoethanol 2%, pH 6.8), centrifuged at 10000 rpm/10 min and the supernatant stored at -18°C. The protein samples (20 μ g per lane) were run in a SDS-PAGE gel electrophoresis at 50 mA. After, the gels were stained in coomassie blue, dried and exposed to kodak t-mat films for up to seven days.

2. Identification and isolation of allelochemicals

Allelochemicals are released into the environment through root exudation, volatilisation, leaves and residue decomposition. Though, most studies were developed through the screening of fraction of plant extracts or leachates (mostly from leaf) for their effects on seed germination of various crops such as cucumber, sesame seed, tomato, lettuce, wheat, etc. Several laboratory experiments used organic solvents for identification and isolation of chemical substances such as ethanol (Silva, 2010, 2006), hexane (Silva, 2006, 2011), chloroform, ethyl acetate (Silva, 2006; Oliveira 2012). For example, laboratory experiment showed that the acetyl acetate leaves extracts of *Solanum lycocarpum* provided stronger allelopathic activity on root inhibition of receptor plants (Oliveira, 2012). However, according to Inderjit & Dakshini (1995), to obtain ecologically relevant data, the use of organic solvents is not recommended. Moreover, an experiment with natural soil collected beneath the canopy of suspected plants can provide the best evidence for the release of phytotoxic chemicals (Silva, 2012).

3. The concentration of allelochemicals released

Allelochemicals are released and added to the soil over a time period and also continually removed and/or immobilised from the soil solution by plant uptake, adsorption to soil particles, and degradation by microorganisms (Kruse, 2000). However, the actual release rate of allelochemicals from living plants may be difficult to be estimated. The main factors that can alter the rate of production the allelopathic compounds consequently the release compounds are seasonality and plants maturity stages. For instance, the aqueous extracts of plants leaves (*Davilla elliptica* St. Hil., *Diospyros hispida* A.D., *Kielmeyera coriacea* Mart., *Miconia albicans* (Sw.) Triana and *Schefflera vinosa* Cham. & Schltld. Frodin) collected at dry season registered greater inhibition rate on *Lactuca sativa* L. seedling than leaves collected at rain season (Gatti, 2008). The allelopathic effect of leachates of young leaves of *Andira humilis* Mart. on germination and root growth of *Sesamum indicum* L. were beyond to the leachates of mature leaves (Menezes et al., 2008). The allelopathic effect in soil is influenced by factors such as soil pH, organic matter content, nutrient and moisture content (Kruse, 2000). Therefore, to observe the actual release of the allelochemicals, the laboratory experiment could be designed by comparing the allelopathic effect of aqueous plants extract and soil samples collected under the canopy.

4. Allelopathy and competition

The allelopathic effects are depended on the release of a chemical plant in the environment, whereas competition involve removal or reduction of an environmental factor such as water, minerals, light, etc. (Rice, 1974). Primarily, to justify the existence of allelopathy plants can be noticed by field investigation or by observing the growth inhibition zones around and beneath the plants where neighboring plants are suppressed (Inderjit, Callaway, 2003). Field observations by Periotto et al. (2004) suggested to hypothesize that there might be allelopathic effect of *Andira humilis* Mart. on other plant species, since this species form homogenous groups and undermines the establishment of other. However, bare zone can be also misleading. Weidenhamer et al. (1989) pointed out that separating allelopathic effect from resource competition would give better understanding. The authors demonstrated experimentally that

allelopathy and resource competition can be distinguished by the density-dependent test. Rech et al. (?) observed the presence of competition resource between *Fabaceae* trees and the neighbor plants. *Copaifera langdorffii* Desf. (*Fabaceae* family) grow in the biome, and the soil collected below the canopy of the trees proved to have allelopathic effect on *Lactuca sativa* (Silva et al., 2012).

5. Research point of view

Nevertheless, to our knowledge there is scarcity of information relating to allelopathic interaction by higher plants and their understory components in this community.



Figure 2 and 3. The leaves and fruit of *Solanum lycocarpum* St. Hil. (left) and the leaves of *Aristolochia esperanzae* O. Kuntze (right). The pictures were taken in Uruaçu, north region of Goiás, Brazil.



Figure 4 and 5. The tree of *Stryphnodendron adstringens* (Mart.) Coville (left) and the fruit of *Magonia pubescens* St. Hil. (right). The pictures were taken in Uruaçu, north region of Goiás, Brazil.

Cerrado fire cycle

Fire is a common characteristic of the savanna. Its presence is more frequent than any other biome and is considered to be an important ecological factor in cerrado ecosystems. Charcoal fragments found in the soil of cerrado around Brasilia, were evidence that fire was already present in this area at least 1200 years before the arrival of the Portuguese discoverers (Mutch, 2003). Fires often break out during a dry season, but may also commonly occur in the transition from the dry and rainy seasons when lightning is prevalent.

The pattern of soil temperatures in cerrado is not different from other savannas ecosystems, where about 97% of burnt matter belongs to the ground layer vegetation, mainly grasses (Ramos, 2003). Cerrados like any other savannas are typically dry and are prone to accumulations of highly volatile fuels. The distribution of trees and woody elements, featuring the savannas allows the arrival of sunlight at ground level and promotes the development of abundant herbaceous layer forming grassy. These grasses have their leaves and floral parts desiccated in the dry season in the periods of May to September. This material is thin and dry to form a highly flammable fuel (Pivello, 2009). When the lightning is prevalent, the lightning bolt strikes a tree trunk, then the smoke rises from woody fuel, hit the grasses and the fire begins. However, today in many areas, the fires happen at a yearly caused by pasture management though, natural fires are also regularly present in places like Emas National Park and Chapada dos Guimares Park. Fires in the area of Emas National Park can be categorized into: natural fires caused by lightning and anthropogenic factors (accidental and intentional). In the period 1995 to 2003, no report the incidence of lightning storm during dry season (June – August), but the incidence frequently occurred during the months from September to February (França et al., 2007).

At an earlier time, in cerrado biome, a natural fire regime was linked to a native plant *Vellozia flavicans* (*Canela-de-ema*) (Fig. 6). The plant is a flammable resin rich and was assumed to burn naturally under the strong sun in the periods of drought. Pinto et al. (1996) experimented the 2,6% hexane extract of *V. flavicans* root, steam and leaf and demonstrated that they contain diterpenes resin acidic. The terpenes fit

into the fire cycle, since they are hydrocarbon in nature and are rapidly volatilized and burn off the soil (Harborne, 2003). During dry season, the sun reflects its beam in the quartz crystal that is abundant in the region then the light will heat a spot in the *Canela-de-ema* to provoke a natural fire on a regular basis every five years. According to the field observation, another plant named *Bavichia vergilioides* (*semente de sucupira*) which is abundant in the cerrado region, rich in natural oils and burn easily, could be one of the fuel materials to help the spread the fire.

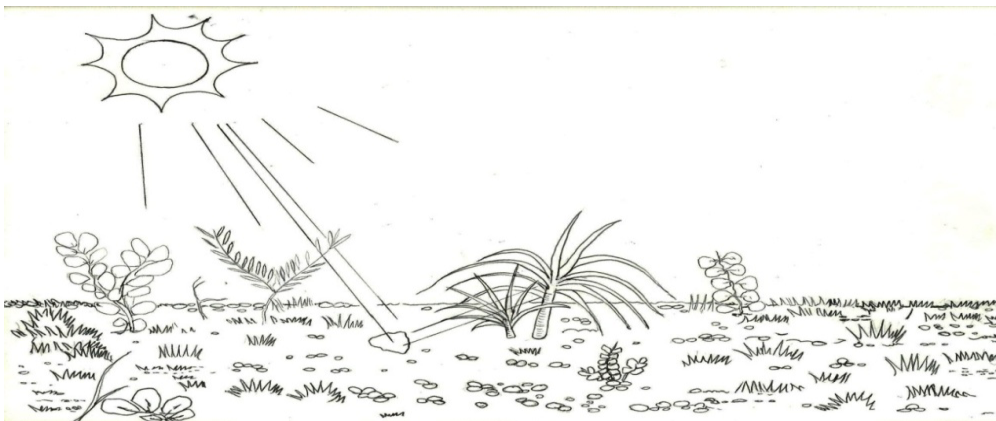


Fig. 6. *Vellozia flavicans* (Canela-de-ema), a native plant, a flammable resin rich. Picture was drawn in the field of Goiás, Brasil.

Post-fire impacts

Coutinho (1982) confirmed that frequent fire favors the maintenance and expansion of savanna formations. Burning causes modification in plant structure and in competition of species.

Burning causes qualitative and quantitative modifications in plant community structure (Souza & Soares, 1983; Eiten & Sambuichi, 1996), in the timing and intensity of flowering (Coutinho, 1982), in population dynamics (Raw & Hay, 1985) and in the competitiveness of species (Viro, 1974), making it possible to select plants with protective structures against fire.

Species	Family		Fire effect	
<i>Heteropterys pteropetala</i> (Adr. Juss.)	Malpighiaceae		seed affected by early fire	Schmidt et al. (2005)
<i>Kielmeyera coriaceae</i> Mart.	Cluciaceae		seed germinated within two weeks following the burning	Cirne & Miranda (2008)

<i>Diospyros hispida</i> A.D.	Ebenaceae		found more in burned area than unburned area in reserved area of cerrado (51:33 individual)	Lucena et al. (2008)
<i>Qualea parviflora</i> Mart.	Vochysiaceae		burned area produced more flowers and fruits	Palermo & Miranda (2012)
<i>Schefflera vinosa</i> (Cham. & Schltldl.) Frodin	Araliaceae		no difference in population observed before and after fire	simposium

Nutrient transfer

Fires, whether they are natural or human made, give importance ecological impacts to cerrado. The fires alter the cycling of nutrients, physical, moisture, and characteristics of the soil. There is an acceleration of remineralization on biomass and nutrients transfer to the soil surface in the ash deposits. During the combustion process, several previously bound nutrients are released in their elemental or radical form. Cations (positive ions) are stable at typical combustion temperatures and remain onsite after burning in the form of ash, when the ash form are leached into the soil, they exchange with H⁺ ions, resulting increase in H⁺ ions in solution and increase the pH of the soil. The higher pH elevates the nutrient cycling of diverse elements critical for plant germinating and growth, including nitrogen and phosphorus (British Columbia, 2004). However, during a fire not all of the nutrients be transferred to the soil surface in the ash deposits, great volume of it are exported to the atmosphere. Fortunately, the nutrient volume exported to the atmosphere will returns back through precipitation processes in three or a little more years. (Continho, 1980).

Changes in vegetation structure and physiognomy

Miranda & Sato (2005) stated that cerrado fires can result in major changes in structure and floristic composition. However, the impacts of fire on plants are dependent on fire frequency, periodicity and intensity. These variables are dependent on abiotic factors such as incidence of lightning strikes and seasonal temperature and precipitation patterns, as well as on certain biotic factors, the plants themselves (Williamson et al., 1992). Fires in cerrado do not cause direct deaths for the established woody plants. Many of the native herbs in shrub lands are adapted specifically to the

fire cycle and can survive high intensity fires with their germination being enhanced various fire effects such as heat and charcoal (Keeley, 1991). With regard to the flora of herbaceous component, studies have shown high resistance to fire and drought, given the types of morphologic and physiologic, and some plants are annuals, developing during the rainy season and most are perennial underground organs as having rhizomes, bulbs and xilopodes that can re-sprout after the fire (Filgueiras, 2002).

Vegetation re-sprouting and flower blooming

Many plant species seem to be favorable by fire for reproduction and flower blooming within a few days or weeks after fire. *Stryphnodendron adstringens* (Mart.) Coville is a good example of this incredible regenerative capacity. In the herbaceous/subshrub, it needs a few days to resume underground organs to sprout, many of its species re-sprouting start with the production of flowers. This stimulus or floral induction is due to complete elimination of the aerial parts of plants that makes them flourish (Jancoski, 2010).

Seed dispersion and germination

Seed of herbaceous and shrub species may germinate readily upon wetting and incubation in the beginning of rain season. In other species, all or portion of the seeds will not germinate unless they receive some particular treatment. Under natural conditions seed of these species may lie dormant in the soil until exposed to temperatures sufficient to stimulate germination (Keeley & Keeley, 1989). This may occur on site devoid of shrubs where soil temperatures can exceed 70°C (Christensen & Muller, 1975) or on burned sites. An example of the germination response to heat was examined by Cirne & Miranda (2008) on native cerrado vegetation in Brazil, *Kielmeyera coriacea* (Clusiaceae) fruit. After a long period of maturation, lasting most of the subsequent dry season, the fruits are totally open and the seeds can be easily detached and dispersed by wind in synchrony with the beginning of the rains (Ribeiro et al., 1985; Cirne & Miranda, 2008). The result showed that the fruit collected before

the fire did not germinate, on the other hand, on the prescribed fire, most fruits opened within two weeks following the burning and 70% of them germinated. By eliminating the dry grass that accumulates on the ground, the fire helps the spread of these species, therefore, removes the weed which prevents or hinders the movement of seeds. There are species in which the head of the seeds is impermeable to water. The sudden and rapid temperature rise in a fire can cause the appearance of cracks in the seed coat and thus make it permeable, favoring their germination (Jancoski, 2010). Cirne & Miranda (2008) also stated that fruit opening on post-fire may occur due to the exposure to the high temperatures that kill living tissues resulting in desiccation and subsequent rending of the fruit structure (Cirne & Miranda, 2008).

Removal of allelopathic compounds

Despite the impacts of high temperatures, high rates of germination can also be achieved by inactivation of inhibitors of germination and/or by the release of chemical compounds necessary for this process. Cerrado is rich of plants which produce secondary metabolite especially phenolic compounds, the group of flavonoids, quercetin and rhamnose. These compounds increase concentration of inhibitory factor in the soil that impedes the germination and plant growth. Many phenolic compounds also form recalcitrant complexes with soil organic nitrogen reducing the nitrogen accessibility to vascular plants. Therefore, the phenol-regulated accumulation of humus and the reduction of nitrogen available for plants inhibit tree seedling establishment and growth (Keech et al., 2005). Muller (1968) stated that in the California chaparral, the leaves of mature *Adenostoma fasciculatum* (Chamise or Greasewood) shrub produce toxin on their surfaces that are leached of the foliage that allelopathically inhibit the germination of herb seed. When fire removes the shrub canopy the herb seeds are released from the inhibitory effect of the allelopathic chemicals. Pietikainen et al. (2000) and Keech et al. (2005) affirmed that fire-produced charcoal is able to regulate soil phenolic compounds released by *E. hermaphroditum* in the European boreal forests.

DISCUSSION

Allelopathy interaction between higher plants or understory components in the cerrado

Complicatedly, the ecological effect of cerrado is characterized by fire, either natural or intentional. The existence of some species that tolerate or are dependent on fire is further evidence that fire has been a major ecological factor in this ecosystem. Post-fire impacts reported in this biome were nutrient transfer, changes in vegetation structure and physiognomy, vegetation re-sprouting, flower blooming and seed dispersion (Miranda & Sato, 2005; Filgueiras, 2002; Jaconski, 2010; Cirne & Miranda, 2008). However, to our knowledge, no study has been referred directly to fire-related impacts on removal of allelochemical concentration from the soil of this community.

Several studies were done in the California chaparral where fires occur with a frequency of once every 10-40 years (Muller et al., 1968, Christensen and Muller, 1975, Keeley and Keeley, 1989). The condition of the soil (compared to cerrado, find similarity). The dense shrubland is dominated by *Adenostoma fasciculatum*. Christensen and Muller (1975) performed experiment of allelopathy and post fire effects. A fire occurring often cause the denature of allelopathic compounds, resulting in a plentiful herbaceous plants appeared during the first growing season in *A. fasciculatum* stand. Under laboratory testing, the aqueous *A. fasciculatum* leaf (rich of phenolic compound) demonstrated a strong inhibition effect on four species: *Lactuca serriola*, *Centaurea melitensis*, *Cryptantha intermedia*, and *Erigeron divergens*. Field observations were done during the study periods showed that these four species inhibited by *A. fasciculatum* were never found under the shrub cover while they germinated or produced new sprout in the first and second years following the fire, in the burned chaparral area. Similar result was obtained following the artificial clearing site. Other factors such as changes of soil moisture, soil texture, and light had little direct effect on postfire germination and growth. However, Keeley & Keeley (1989) confirmed that there is lack of evidences that allelochemicals provide an important role in canopy regeneration and suggested that seed dormancy is the primary factor in the early post-fire succession.

Allelochemicals are released to the soil over a time period and also continually removed from the soil solution by plant uptake, adsorption to soil particles, and

degradation by microorganisms (Cheng 1995, Kruse, 2000). The actual release rate of allelochemicals from living plants may be difficult to calculate but the estimation of chemical concentration removed by fire might be performed.

Regarding to an understanding that fire has been a major force in maintaining the characteristic structure and composition of the cerrado ecosystem, therefore, the need of fire management implication is an urgent. An intentional controlled fire can be set within a restricted area, with heat intensity and fire spread to meet the management objectives. Ramos (2003) suggested that different strategies have to be applied to establish an appropriate fire regime by maintaining size, rotation and burnings techniques.

CONCLUSION

Studies demonstrated that many vegetations of cerrado region produced allelochemicals. The compounds present in roots, leaves, seeds, flowers, rhizomes, stems and pollen of plants pollute the soil and can influence the growth of other plants or its understory. Many authors confirmed that fire regime whether natural or human-made plays a key role to remove the allelochemicals effects from the soil. Fire produced charcoal, is able to regulate soil phenolic compounds released by toxic herbs. However, it is still difficult to point out that allelopathy is the most responsible factor for seedling survival and plants regeneration on cerrado vegetation. More work is needed on post-fire impacts that refer to allelopathic plant and their competitors in this biome.

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