Contribution to the discussions on the origin of the cerrado biome: Brazilian savanna

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Abstract

Theories that attempt to explain the origin of the cerrado biome are mostly based on the isolated action of three major factors: climate, fire and soil. Another factor that has been mentioned is that of human interference. We hypothesise that the evolutionary origin of this biome resulted from the complex interaction of climate, fire and soil, with climate being the triggering agent of this assumed interaction. Fire, as well as acid and dystrophic soils, would be factors involved in the selection of savanna species throughout climatic events, during the Tertiary and the Quaternary, e.g. Pliocene and Pleistocene. The genesis of the physiognomies that would give rise to cerrado sensu lato, rather than forest formations, could have occurred due to the strong pressure exerted by the reduction in water availability, and the selection of the species adapted to the new conditions imposed by the environment. The characteristics of cerrado sensu lato soil, originated from edaphic impoverishment caused by lixiviation and successive past fires, would remain, even after hydric availability increased following the Pleistocene glaciations.

Keywords: climate, fire, ecotypes, refugia, soil.

Contribuição às discussões sobre a origem do bioma cerrado: savana brasileira

Resumo

Teorias que tentam explicar a origem do bioma cerrado baseiam-se, principalmente, na ação isolada de três fatores principais: o clima, o fogo e o solo. Outro fator mencionado ainda é a interferência humana. Quanto à origem evolutiva desse bioma, o presente estudo propõe uma hipótese que considerou a complexa interação dos três primeiros fatores, mencionados acima, considerando o clima como elemento desencadeador dessa possível interação. O fogo e solos ácidos e distróficos teriam atuado como fatores de seleção de espécies savânicas, ao longo das oscilações climáticas durante o terciário e o quaternário, e.g. Plioceno e Pleistoceno. A gênese das fisionomias que passariam a compor o chamado cerrado sensu lato, em detrimento de formações florestais, teria resultado da forte pressão exercida pela redução da disponibilidade hídrica e da seleção de espécies adaptadas às novas condições impostas pelo ambiente. As características do solo, que passariam a manter o cerrado sensu lato, oriundas do empobrecimento edáfico pela lixiviação e sucessivos incêndios pretéritos, permaneceriam, mesmo com o restabelecimento de uma maior disponibilidade hídrica, após as glaciações do Pleistoceno.

Palavras-chave: clima, fogo, ecótipos, refúgios, solo.

1. Introduction

The origins of the cerrado biome, which occupies approximately 2 million km² of the Brazilian territory, bordered by the Amazon and the Atlantic Forests (Ratter et al., 1997; Oliveira Filho and Ratter, 2002), is still a matter of debate (Ribeiro and Walter, 1998; Ledru, 2002). Several theories have been proposed to explain its formation (Alvin, 1954; Cole, 1960; Fernandes, 2000; Oliveira Filho and Ratter, 2002), including the possibilities of natural or anthropogenic origin (Ledru, 2002). The best known theories support the notion that the origin of

cerrados is related to the influence of climate (Warming and Ferri, 1973), soil (Alvin, 1954) and fire (Rawitscher, 1951; Coutinho, 1990).

The distribution of cerrado and, particularly, the factors that contributed to its origin and permanence (Fernandes, 2000), have been widely discussed. The advocates of pyrogenic origin (Rawitscher, 1951) question the climatic hypothesis by pointing out, for example, that cerrados and forest formations have co-existed under the same climatic conditions, and that xerophytism

alone could not be deemed responsible for the creation of cerrados (Alvin, 1954). On the other hand, the pyrogeny hypothesis is criticised for considering cerrado sensu stricto as a secondary formation derived from cerradão due to the action of fire. According to the opponents of this hypothesis, it could not be true because, in many regions of cerrado, the occurrence of cerradão would not be possible due to the fact that its edaphic, hydrologic and topographic conditions are unsuitable for such a forest-like savanna physiognomy (Fernandes, 2000).

South America underwent climatic changes in different geologic epochs (Cruz Júnior et al., 2005) e.g., the Pliocene and Pleistocene (Rull, 2008). At the end of the Tertiary and throughout the Quaternary periods, changes in landscape occupation (Raven and Axelrod, 1974) favoured the formation of either savannas or forests, depending on whether environmental wetness decreased or increased, respectively (Gottsberger and Morawetz, 1986; Ribeiro and Walter, 1998; Furley, 1999; Scheel-Ybert et al., 2003).

Savanna fires had certainly occurred long before the arrival of humans in South America. The oldest palynologic record of cerrado flora, found in the Brazilian Central Plateau, dates back approximately 32,000 years B.P. (Ledru, 2002). Cerrado vegetation had probably already developed adaptation to fire by that time, which preceded any known human activity (Scheel-Ybert et al., 2003). Charcoal remains from different time periods, including some from the late Quaternary (Ledru, 2002), have been found in different Brazilian regions (Behling, 2002; Gouveia et al., 2002; Behling, 2003; Scheel-Ybert et al., 2003), testifying the occurrence of natural, possibly frequent, fire (Behling, 2003), which in turn might have influenced the local floristic composition (Behling, 2002), while water availability affected the predominant physiognomy (Vivo and Carmignotto, 2004).

The information provided by Ferri (1979) on the evolutionary and successional origin of cerrado is very important, especially when fire and anthropic actions are considered as contributory elements to the formation of this kind of vegetation.

Based on recently acquired scientific data, this study aimed at addressing important questions concerning the evolutionary origin of the cerrado biome and its physiognomies – campo limpo, campo sujo, campo cerrado, cerrado sensu stricto, cerradão (Lock, 2006) – by proposing hypotheses about the development of one of the most complex Neotropical plant communities, through the combined action of climate, soil and fire.

2. Floristic and Paleontologic Evidences

The distribution of past savanna formations over several Neotropical regions could be inferred from paleontological records (Ranzi, 2000; Gouveia et al., 2002; Behling, 2002; Behling, 2003; Scheel-Ybert et al., 2003; Vivo and Carmignotto, 2004). Fossils of terrestrial animals alongside palynological records have confirmed the existence of large Neotropical savannas during the Quaternary period (Ranzi, 2000; Van der Hammen and Hooghiemstra, 2000). These records are usually associated with climatic changes defined by periods of greater or lesser water availability (Ribeiro and Walter, 1998; Cruz Júnior et al., 2005). Some of these records, such as the ones on areas presently occupied by the Amazon and Atlantic rainforests, indicate an increased occurrence of savannas during extreme climatic conditions, i.e., accentuated rainfall decline (Gottsberger and Morawetz, 1986; Ledru, 2002). The advance of glaciers in temperate regions at different periods resulted in the development of xerophile formations, such as savannas, in tropical and subtropical areas (Raven and Axelrod, 1974; Goldblatt, 1978; Siffedine et al., 2004; Pennington et al., 2006). The abundance of herbaceous species due to the absence or low density of shrub and tree individuals is characteristic of open savannas such as campo limpo and campo cerrado (Ribeiro and Walter, 1998). This feature was a determinant factor for the emerging and maintenance of the Quaternary period megafauna, especially throughout the Pleistocene (Ranzi, 2000), that started in approximately 2.5 m.yr. B.P.

The records of animal fossils on sediments formed during the Quaternary glacial periods, allowed the paleoecologic reconstruction of savanna environments (Ranzi, 2000; Vivo and Carmignotto, 2004), making possible even a description of the food chains that had herbaceous species, which are so abundant in savannas (Vivo and Carmignotto, 2004), as primary producers. These herbaceous plants were an important source of food for large herbivores, such as *Toxodon*, *Glyptodon*, and *Haplomastodon* the majority of which were grazers that inhabited open areas (Ranzi, 2000). The leading role played by herbaceous plants in the food chain has been associated with the extinction of Neotropical mammals, in the hypothesis proposed by Vivo and Carmignotto (2004). According to these authors, forest expansion was crucial for the extinction of Neotropical megafauna that depended on extensive open grassland. Thus, Vivo and Carmignotto (2004) considered that Quaternary climatic events (Auler et al., 2004; Wang et al., 2004) influenced Neotropical floristic changes, in opposition to the theory of taxa extinction of this tropical megafauna due to direct competition with mammalian species originated from the American continent temperate regions that reached South America through the newly formed Panama isthmus (Webb, 1991).

Recurrent Neotropical dryness, a consequence of the Quaternary climatic events (Fernandes, 2000), favoured the increase of savannas in that region between the Miocene and Pleistocene epochs. Some plant groups, such as Asteraceae, that efficiently occupied Neotropical savannas (Raven and Axelrod, 1974), were favoured by the lower seasonal water availability characteristic of these formations. The increase in sclerophyll plants was enhanced by speciations from forest ecotypes of wide

dispersion that became adapted to water-restricted environments (Rizzini, 1997).

The Quaternary climatic events would have provided favourable conditions (Van der Hammen and Hooghiemstra, 2000) for the diversity of caatinga and cerrado that emerged at some point during the Quaternary period (Oliveira Filho et al., 2006; Queiroz, 2006) or, perhaps even sooner, during the Tertiary (Raven and Axelrod, 1974; Queiroz, 2006). Thus, sympatric speciations gave rise to vicariant species from forest ecotypes (Rizzini, 1997) of a fragmenting vegetation matrix (Pennington et al., 2000). These ecotypes must have overcome the restrictions imposed by the drier climate which in turn, must have strongly restrained the distribution of forest species throughout the cerrado (Méio et al., 2003). According to Allem (2004), an example of sympatric speciation among cerrado Euphorbiaceae (under edaphic influence, in this case) involved *Manihot violacea* Pohl as the parent species and *M. irwinii* D.J. Rogers & Appan as the derived species.

Nevertheless, Cole (1960) considered forests and caatinga as being more recent than savannas. However, the assumption that cerrado originated from forest species sounds reasonable, and has been corroborated by Webb (1978), according to whom areas covered by rich wet forest formations were found in the Neotropical region during the Paleocene, and open shrubby savannas, consisting of abundant gramineous elements, would have later differentiated from the still large wet forests, i.e., during the Middle Eocene (Pennington et al., 2006). In addition, assuming that Gramineae and Cyperaceae species have always dominated the herbaceous layer of savannas worldwide (Solbrig, 1996), a cerrado sensu lato physiognomy lacking the presence of these herbaceous species would be inconceivable. Therefore, given that the oldest paleontologic records of Gramineae and Cyperaceae go back to Paleocene and Eocene (Cronquist, 1993), and that the greatest diversification of Gramineae species would have occurred during Oligocene and Miocene (Jacobs et al., 1999), cerrado proto-physiognomies must have arisen approximately 38 m.yr. B.P. (Jacobs et al., 1999), and not before. Paleontologic records indicate that wet tropical forests were already present in South America and Africa during Paleocene (Goldblatt, 1978; Jacobs et al., 1999).

The emergence of vicariant savanna species derived from forest species, e.g., *Aegiphila lhotskiana* Cham., *Agonandra brasiliensis* Miers ex Benth. and Hook. f., *Andira humilis* Mart. ex Benth., *Aspidosperma tomentosum* Mart., *Caryocar brasiliense* Cambess., *Dimorphandra mollis* Benth., *Plathymenia reticulata* Benth., *Sclerolobium aureum* (Tul.) Baill. and *Terminalia fagifolia* Mart. (Rizzini, 1971; Heringer et al., 1977), commonly found in cerrado (Ferri, 1977), could have resulted from the occupation of new environments by groups (Stace, 1991) originating from the retraction of wet forests, parallel to the expansion of open vegetations, such as campo cerrado and caatinga, from wet forest refugia during Holocene climatic events (Fernandes, 2000). In this manner, a great number of vicariant species originated from wetter forest formations, could have developed in savanna areas and become a peculiar floristic element, evolving in loco toward a constant morphological pattern, i.e., small size, thick and pileous leaves, thicker rhytidomes. However, these characteristics as well as others do not always occur together, but rather in a combined manner (Rizzini, 1971).

Other evidence concerning the occurrence of xeric formations and the importance of recurrent dry periods in the Neotropical region, include the adaptation of plant groups to these new environments occupying different dry plant formations. Examples of caatinga floristic elements that may occur in cerrado are: *Amburana cearensis* (Allemão) A.C. Sm., *Commiphora leptophloeos* (Mart.) J.B. Gillett, *Jatropha urens* L., *Maytenus rigida* Mart., *Mimosa caesalpiniifolia* Benth., *Piptadenia moniliformis* Benth. *Solanum oocarpum* Sendtn. (Rizzini, 1997; Mendonça et al., 1998; Prado, 2000). Other species may be found in both savannas and dry forests: *Agonandra brasiliensis* Miers ex Benth. and Hook. f., *Bauhinia cupulata* Benth., *Cassia ferruginea* (Schrader) Schrader ex DC., *Clusia burchellii* Engl., *Machaerium scleroxylon* Tul., *Miconia macrothyrsa* Benth., *Myracrodruon urundeuva* Allemão, *Poiretia elegans* C. Mueller and *Physocalymma scaberrimum* Pohl (Mendonça et al., 1998; Ribeiro and Walter, 1998).

3. The Complex Interaction among Abiotic Factors

In the Neotropical regions during the Quaternary period, there were periods of high annual precipitation followed by the expansion of forest formations. Before that, these formations were restricted to damper refugia, such as the bottom of valleys, and following water courses (Webb, 1991; Van der Hammen and Hooghiemstra, 2000; Pennington et al., 2000). These forest formations probably remained linked to each other through the dendritic network within the cerrado (Ranzi, 2000), formed by the existing forests (Ledru, 2002), maintained by the soil with greater water availability (Oliveira Filho and Ratter, 2000; Oliveira Filho and Ratter, 2002), and sheltered against more intense fire actions by the increased humidity and litterfall of such forests (Eiten, 1972; Lindenmayer et al., 1999), as well as the type of fuel produced by them (Biddulph and Kellman, 1998).

It is then possible that, during the Quaternary glacial periods, areas relatively close to water courses, where efficient water retention could be achieved – either due to clay accumulation or lower soil depth (Resck and Silva, 1998; Silva Júnior et al., 1998) formed refugia for seasonal deciduous and semi-deciduous forests, despite low water availability. That hypothesis can be confirmed by evidence presented by Ledru (2002). Thus, vegetal formations similar to the valley forests found in the cerrado (Oliveira Filho and Ratter, 2002) would have arisen.

Favier et al. (2004) corroborated the hypothesis of forest micro-refugia in riparian zones where savanna predominated with computer simulations.

The complex distribution of different sites according to hydric availability on soils with distinct characteristics, e.g. fertility (Silva Júnior et al., 1998), could have favoured the maintenance of microenvironments defined by differences in drainage systems, production and accumulation of litterfall, and topographic variations (Correia et al., 2001), among others. Such sites could have been suitable for parapatric speciations (Svenning, 2001) along edaphic and topographic gradients (Gentry, 1982) from forest species ecotypes that started to differ morphologically during the colonisation of those microenvironments (Stace, 1991). It is possible, for example, that savanna species belonging to the Chrysobalanaceae family emerged from adaptive mechanisms culminating in speciations, as described above (Prance, 1992).

Other types of forest remnants could have occurred in Quaternary savannas. Such remnants possibly shared the same characteristics seen in the so-called upland forests (brejos de altitude) presently found in the caatinga in northeastern Brazil after the retraction of forest remnants from the vast wet forest matrix that dominated the Cretacean landscape (Fernandes, 2000). In upland forests, precipitation is high due to the influence of condensation mechanisms that are likely to be similar to those found in the Amazon forest (Silva Dias et al., 2001) despite the lower hydric availability in the surrounding caatinga (Cabral et al., 2004; Tabarelli and Santos, 2004). Thus, during the Quaternary period, higher plateaus could have locally concentrated precipitations that preserved local wetness (Oliveira Filho and Ratter, 2000; Pennington et al., 2000) and favoured the existence of forest formations.

The forest retraction caused by the reduced rainfall could have triggered a series of environmental changes, e.g., impairment of nutrient cycling due to decreased litterfall production. However, even the occasional rains would have been sufficient to increase edaphic acidity, carrying considerable amounts of exchangeable bases from the soil surface layers, increasing not only acidity but also the concentration of aluminum, which is toxic for vegetal individuals (Sarmiento, 1984). A number of cerrado species have developed the ability to accumulate edaphic aluminium, such as *Qualea multiflora* Mart. and *Vochysia thyrsoidea* Pohl (Haridasan, 1982), as well as some species of the genera *Neea* Ruiz and Pav., *Strychnos* L., *Miconia* Ruiz and Pav., *Psychotria* L., *Roupala* Aubl. e *Palicourea* Aubl. (Ferri, 1977).

It seems reasonable to infer that, during the Holocene, as wetness was restored to the cerrado region, the lixiviation process became more intense (Furley, 1999), promoting the expansion of cerrados and the retraction of mesophytic forests which never regained the rich and extensive forest cover it had during the Pliocene (Raven and Axelrod, 1974), not even as precipitation increased (Oliveira Filho and Ratter, 2000). During this time, for-

ests were at a competitive disadvantage against savannas in the occupation of the soil impoverished by lixiviation in some regions.

The woody plant species that started to occupy this environment mostly originated from forest formations in the Amazon and Atlantic basins (Oliveira Filho and Ratter, 2000) by vicariant mechanisms (Rizzini, 1971; Heringer et al., 1977), and contributed to the development of a rich and complex savanna flora that included endemic species (Franco, 2002). The floristic elements occupying this developing environment underwent adaptations to factors that initially included decreased wetness availability and increased edaphic acidity and toxicity and, at a later stage, increasingly frequent fires (Furley, 1999). For Raven and Axelrod (1974), the recurrent dry cycles that took place in the tropics during glaciations, could more plausibly explain the expansion of tropical savannas than man-made fires.

It is currently accepted that the distribution of cerrado vegetation across the Neotropical region occurred under the influence of a group of concurrent environmental factors. The impact of these factors varied according to environmental characteristics such as seasonal precipitation, low soil fertility, fires and even the Quaternary climatic changes (Oliveira Filho and Ratter, 2000; Oliveira Filho and Ratter, 2002). The interaction among the above factors should also be considered to have imposed a strong selective pressure on cerrado plant species, and plays a critical role in the establishment and development of the plant community characteristics. Nevertheless, the reduction in environmental wetness availability would indeed be the factor that triggered the evolutionary mechanisms responsible for the establishment of this new savanna flora. Neotropical dryness that peaked during the better part of the Quaternary period, favoured the occurrence of fires, which in turn contributed to soil impoverishment by volatilising edaphic nutrients (Kauffman et al., 1994; Oliveira Filho and Ratter, 2002).

Some ecological features of the cerrado biome seem to support the hypothesis of interaction among environmental factors presented above. Fire and drought, as well as herbaceous root systems competing for nutrients and water, limit the growth of small woody species in Neotropical savannas (Medina and Silva, 1990). Thus, the chance of surviving in the cerrado among small shrubby trees would depend on their ability to drain water from the soil surface layers, maintain underground energy reserves, and keep growing despite fires and dry seasons (Franco, 2002). Fire suppression can increase the chance of survival of small plants of some species such as *Axonopus canescens* (Nees ex Trin.) Pilg., *Miconia albicans* (Sw.) Triana and *Roupala montana* Aubl (Hoffman, 1998; Miranda et al., 2002).

Perennial herbaceous species account for 95% of the herbs found in cerrado. Their radicular systems, which are deeper than those of the annual species, place them at an advantageous condition in the competition for water (Axelrod, 1972; Filgueiras, 2002) in deeper horizons,

where hydric availability is more constant, even during dry seasons (Franco, 2002). Most evergreen and annual herbaceous plants are highly fire-resistant. Some of the annual herbaceous species grow exclusively during rainy seasons, which allow their seeds to avoid fires and drought (Coutinho, 1990). Some annual and evergreen gramineous species, however, respond differently to changes in fire frequency. Annual grasses, like *Andropogon brevifolius* Sw., are more capable of enduring frequent fires than perennial species like *Andropogon semiberbis* (Ness) Kunth (Silva, 1996). Annual or ephemeral (Monasterio and Sarmiento, 1976) species resist fire and drought by storing their seeds in the soil. According to these authors, this may have resulted from the climatic events that occurred during the Quaternary period.

Grime (1979) seems to corroborate the efficiency of the annual plants in occupying environments prone to catastrophes, such as fire, by suggesting that persistent seed banks would permit the quick occupation of the landscape after these events. Short stability periods would suffice for the evergreen herbaceous layer to reoccupy the environment. In fact, several evergreen herbaceous plants are favoured during savanna post-fire occupation, e.g. the African gramineous species *Melinis minutiflora* P. Beauv. (Hoffman et al., 2004).

Fire is crucial in determining the composition and the structure of woody and herbaceous community (Hoffmann, 1998; Oliveira Filho and Ratter, 2002). However, it is not the only influencing factor. Other factors, such as low edaphic nutritional quality, shallow soil, among others (Coutinho, 1990), might define savanna physiognomies commonly related to frequent fire regimes. Fire tends to favour vegetative reproduction by means of underground structures as a strategy for some woody species to survive in fire-prone environments (Hoffmann, 1998), e.g., *Echinolaena inflexa* (Poir.) Chase (Miranda et al., 2002). In the cerrado, fire occurs at surface level and consumes the accumulated litterfall and herbaceous plants (Miranda et al., 2002). Some woody species apparently benefit from fire action blossoming right afterwards (Coutinho, 1990), while others seem to depend on fire for sexual reproduction. Among herbaceous plants, intense fire-stimulated blossoming is observed (Miranda et al., 2002). However, a negative impact has been reported on fruit and seed production in *Miconia albicans* (Sw.) Triana, *Piptocarpha rotundifolia* (Less.) Baker and *Roupala montana* Aubl. (Hoffman, 1998).

According to Franco (2002), environments showing high photosynthesis rates and low nutrient availability, such as Neotropical savannas, would favour an elevated accumulation of carbon in the biomass produced by the radicular system, as well as the establishment of mutualism with mycorrhizal fungi to improve soil nutrient uptake in several cerrado species. Sclerophylly is commonly seen in cerrado woody plants (Franco, 2002), resulting in larger production of roots (Abdala et al., 1998; Franco, 2002). Such a mechanism might also be related

to the competitive interaction between woody plants and herbaceous superficial roots (Abdala et al., 1998). Among the factors reported above, the high accumulation of carbon found in the nutrient-poor scleromorphous leaves of cerrado shrubby tree species (Franco, 2002), alongside suberisation on stems and branches, an effective thermal insulator for living tissues during fire action (Miranda et al., 2002), support the theory of oligotrophic scleromorphism (Arens, 1958).

The high investment made by savanna species in the production of a developed radicular system able to ensure the better use of water, even during dry seasons (Franco, 2002; Hoffman and Franco, 2003), seem to provide evidence of past hydric restrictions caused by climatic influences in the evolution of Neotropical savannas from forest communities.

4. Conclusions

The influence of climatic and edaphic factors alongside periodical fire on the occupation of forest and savanna formations located in the same region is an argument shared by several authors (Oliveira Filho and Ratter, 2000; Oliveira Filho and Ratter, 2002; Coutinho, 2002). However, the relative importance of these factors on the biology of savanna plants remains to be elucidated. A larger number of questions arise when speculations on the results of the combined action of these abiotic factors are made.

Whenever the origin and evolution of the cerrado biome are discussed, the interaction among climatic events, physical-chemical properties of the soil, and fire action should be considered of paramount importance for the understanding of distinct evolutionary mechanisms such as gradual speciation through local adaptation (Stace, 1991). Studies addressing similar phenomena might propose evolutionary hypotheses that can help explain the emergence of different cerrado plant groups.

Both fire and dystrophic soil might have been important selective agents, defining a flora adapted to environments of lower hydric availability, gradually shaped by the climatic events that took place in the Quaternary. Nonetheless, climate is the triggering factor, that is, the one that allowed the occurrence of frequent fires and edaphic impoverishment.

The fact that climate seasonability alone could not explain the current predominance of savanna formations, in areas where wetness is sufficient for the establishment of forest formations (Gottsberger and Morawetz, 1986), should be considered. In some of these areas, the transition of forest formations to cerrado seems to be related to edaphic factors rather than to fire action (Ratter, 1992). In addition to edaphic factors, other abiotic factors might play a role in defining the distribution of savanna and forest formations (Oliveira Filho and Ratter, 2002), e.g., regional hydrologic and topographic characteristics (Fernandes, 2000).

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