

Potential impacts of climate change on biogeochemical functioning of Cerrado ecosystems

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(With 2 figures)

This paper is dedicated to the memory of our friend Dr. Julio Carlos França Resende

Abstract

The Cerrado Domain comprises one of the most diverse savannas in the world and is undergoing a rapid loss of habitats due to changes in fire regimes and intense conversion of native areas to agriculture. We reviewed data on the biogeochemical functioning of Cerrado ecosystems and evaluated the potential impacts of regional climate changes. Variation in temperature extremes and in total amount of rainfall and altitude throughout the Cerrado determines marked differences in the composition of species. Cerrado ecosystems are controlled by interactions between water and nutrient availability. In general, nutrient cycles (N, P and base cations) are very conservative, while litter, microbial and plant biomass are important stocks. In terms of C cycling, root systems and especially the soil organic matter are the most important stocks. Typical cerrado ecosystems function as C sinks on an annual basis, although they work as source of C to the atmosphere close to the end of the dry season. Fire is an important factor altering stocks and fluxes of C and nutrients. Predicted changes in temperature, amount and distribution of precipitation vary according to Cerrado sub-regions with more marked changes in the northeastern part of the domain. Higher temperatures, decreases in rainfall with increase in length of the dry season could shift net ecosystem exchanges from C sink to source of C and might intensify burning, reducing nutrient stocks. Interactions between the heterogeneity in the composition and abundance of biological communities throughout the Cerrado Domain and current and future changes in land use make it difficult to project the impacts of future climate scenarios at different temporal and spatial scales and new modeling approaches are needed.

Keywords: Savanna, nutrient cycling, fire, land use, climate change, carbon.

Os impactos potenciais das mudanças climáticas no funcionamento biogeoquímico dos ecossistemas de cerrado

Resumo

O Domínio Cerrado é composto por uma das savanas mais diversas do mundo e está passando por uma rápida perda de habitats devido às mudanças nos regimes de fogo e intensa conversão de áreas nativas para a agricultura. Os dados sobre o funcionamento biogeoquímico do Cerrado foram revisados, avaliando-se os potenciais impactos das mudanças climáticas regionais. As variações na temperatura, na precipitação e altitude ao longo do Cerrado determinam diferenças marcantes na composição das espécies. Os ecossistemas de Cerrado são controlados por interações entre a água e a disponibilidade de nutrientes. Em geral, a ciclagem de nutrientes (N, P e cátions) são muito conservadores, enquanto a serapilheira, a biomassa microbiana e vegetal são importantes compartimentos de estoque. Em termos de ciclagem de C, o sistema radicular e, especialmente, a matéria orgânica do solo são os estoques mais importantes. Em bases anuais, o ecossistema de cerrado típico funciona como sumidouros de C embora opere como fonte de C para a atmosfera ao final da estação seca. O fogo é um fator importante alterando os estoques e fluxos de C e nutrientes. As previsões de mudanças na temperatura, quantidade e distribuição da precipitação variam de acordo com as sub-regiões do Cerrado,

com mudanças mais acentuadas na parte nordeste do domínio. As temperaturas mais elevadas, diminuição da precipitação com o aumento da duração da estação seca, podem deslocar as trocas líquida do ecossistema de dreno para a fonte de C e podem intensificar as queimadas, reduzindo os estoques de nutrientes. As interações entre a heterogeneidade na composição e abundância das comunidades biológicas ao longo do Domínio Cerrado com as mudanças atuais e futuras do uso da terra tornam difícil a projeção dos impactos dos cenários climáticos futuros em diferentes escalas temporais e espaciais e novas abordagens de modelagem são necessárias.

Palavras-chave: Savana, ciclagem de nutrientes, fogo, uso da terra, mudanças climáticas, carbono.

1. Introduction

The Cerrado Domain covers approximately 2 million km² of the Brazilian Central Plateau (24% of the country's total area) and is the second largest phytogeographic province in Brazil sharing transitions with other Brazilian Domains: the Amazon Forest, Caatinga, Pantanal and Atlantic Forest. The region encloses the headwaters of three major South American basins: Tocantins-Araguaia, Paraná-Prata and São Francisco (Felfili and Silva Junior, 2005). It is one of the richest and most diverse savannas in the world (Lewinsohn and Prado, 2005) and is considered as one of the 34 global hotspots of biodiversity (Mittermeier et al., 2005) because of the high level of endemism and rapid loss of habitats due to changes in fire regimes and intense conversion of native Cerrado to pasture and cropland.

In this paper, we reviewed the literature on biogeochemical functioning of Cerrado ecosystems and the effects of disturbances such as fire and deforestation on their functioning. These aspects are then evaluated in conjunction with the modeled changes in climate for the region.

2. The Cerrado Domain

2.1. Characterization of Cerrado ecosystems

The Cerrado has a wet seasonal climate, with precipitation ranging from 800 to 1,800 mm, with about 90% of the annual precipitation occurring during the rainy season, between October and April. The dry season lasts from 4 to 7 months. The large geographic distribution of the Cerrado and the highly variable topography (ranging from almost sea level to over 1,300 m) lead to a large range of temperatures across the area (Eiten, 1972). Although the annual mean temperature varies from 20 to 26 °C across the Cerrado, temperature extremes are remarkably different. The minimum temperature in the southern part of the Cerrado (São Paulo state) reaches -4 °C, while the minimum temperature in the northern part (Piauí state) reaches 14 °C. The range of temperature variation throughout the year is also remarkably different within the Cerrado. In the northern part of Piauí, for example, variation during the year is around 22 °C while in the southern part of São Paulo this variation reaches 44 °C.

The amplitude of temperature across the Cerrado, coupled with differences in precipitation and altitude determines marked differences in the composition of species. Three regional centers of biodiversity in the Cerrado: Southeastern Cerrado, Northeastern Cerrado and Central Cerrado were

identified and are related to the polygons of drought and frost and different altitudinal ranges (around 400 to 500 m or 900 to 1,000 m) (Castro, 1994). Ratter et al. (2003) characterized the Cerrado diversity in five core regions: Central and southeastern, central-western, far western mesotrophic sites; North and Northeastern, Southern.

The Cerrado landscape is composed of a vegetation mosaic ranging from grassland to forest formations differing from each other in structure and composition and levels of deciduousness (“*campo limpo*” - grassland, “*campo sujo*” - grassland with scattered trees, “*cerrado sensu stricto*” - savanna - typical cerrado, and “*cerradão*” - woodland) (Ribeiro and Walter, 1998). Gallery forests (evergreen formations that follow streams) are found throughout the region occupying ~5% of the Cerrado area but containing approximately 32% of its biodiversity. The Cerrado has the highest plant diversity among tropical savannas with ca. 12,000 species of angiosperms (Mendonça et al., 2008). The herbaceous layer of Cerrado areas present a greater representation of Fabaceae (~780 species) followed by Asteraceae (~560 species), Poaceae (~500 species) and Orchidaceae (~495 species) (Filgueiras, 2002). In terms of soil cover, there is a predominance of grasses (Munhoz and Felfili, 2006).

Oxisols is the predominant soil type covering 45% of the Cerrado region while Entisols cover approximately 15% (Reatto et al., 1998). These soils have low surface charge and low nutrient content. Under natural conditions, the availability of nutrients in the weathered Cerrado soils is dependent on the mineralization of organic matter, where litter decomposition rates are described as slow, with half-life greater than one year (Silva, 1983; Constantino, 1988; Kozovits et al., 2007). Studies in the Cerrado have shown that the dominance of woody/grass vegetation could be determined by the availability of nutrients and water, soil aluminum and acidity, fire regime and waterlogging (see Oliveira and Marquis, 2002).

2.2. Phenology and functioning of Cerrado ecosystems

The marked seasonality of savanna ecosystems is well represented in the phenology of their communities. Growth events tend to be relatively short, with peaks of intensity in different periods of each season (Lenza, 2005; Lenza and Klink, 2006). In typical cerrado plant communities, despite the relative homogeneity of soils and climate, different strategies of leaf phenology can be observed (Franco, 2002; Lenza, 2005; Araújo and

Haridasan, 2007). A common feature is the pronounced seasonal character of the evolution of events (Lenza, 2005; Lenza and Klink, 2006).

Instead of discrete phenological groups, what has been observed in the field is a continuum of strategies for leaf phenology, ranging from deciduous, brevi-deciduous to evergreen species, with varying degrees of intensity and duration of deciduousness (Goldstein et al., 2008). Much more than just intensity and duration of shedding, phenological groups have other functional differences. There are not only differences in the patterns of water uptake between deciduous and evergreen trees, but also species-specific differences among evergreen trees (Jackson et al., 1999), that have implications for regulation of tree water balance (Goldstein et al., 2008). In addition to these differences many trees have dimorphic root systems with both deep and shallow roots (Goldstein et al., 2008).

Specific leaf area (SLA, i.e. proportion of leaf area per unit of leaf mass) has also been identified as a functional difference between phenological groups of typical cerrado). Studies have shown correlation of both mass-based maximum CO₂ assimilation and SLA, with higher concentrations of N and P. This suggests that savanna species with lower SLA invest more in structural components than in metabolism. In addition, there are studies indicating that species with lower specific leaf area have greater leaf longevity. Thus, there is a trade-off: species with higher SLA have the advantage of rapid production of biomass, but are less efficient in the conservation of nutrients from leaves (Franco et al., 2005; Araújo and Haridasan, 2007).

The contents of nitrogen and phosphorus in the leaves are also functional differential aspects of phenological groups, and are important indicators of nutritional status of woody plants (Nardoto et al., 2006). In typical cerrado communities, the difference between phenological groups decreases with the progress of the rainy season (Araújo and Haridasan, 2007). The following groups are characterized according to the classification used by Lenza (2005): Evergreen with continuous growth: Species with slight decreases in the percentage of intensity crown cover (PICC), with values above 80% during the year. The production of new leaves takes place continuously and there is not a well defined period of leaf exchange; Evergreen with seasonal growth: while maintaining PICC values similar to evergreen with continuous growth, the species of this group have a short, well-defined leaf exchange. Production of the new cohort of leaves and fall of the cohort of old leaves are temporally close if not simultaneous. There is a peak near the transition drought/rain, with strong synchrony among individuals; Brevi-deciduous: species completely replace the foliage during the dry season. However, PICC remains below 10% for a short period of time (up to three weeks), followed by intense leaf production and full recovery of the crown area just before the start of the rainy season; Deciduous: Like the Brevi-deciduous, the Deciduous species completely lose foliage during the second half of the dry season. The difference between the two functional groups is the intensity of PICC at less than 10%. Species

of this group may remain without leaves or with a few leaves for a period longer than one month, after which there is intense sprouting and recovery of canopy cover.

Both evergreen groups have common functional characteristics: comparing to deciduous, evergreen species tend to have lower SLA, therefore lower maximum CO₂ assimilation and leaf nutrient content than deciduous species. The leaves can last for over a year and seasonality in leaf nutrient concentration is not significant (Franco et al., 2005; Araújo and Haridasan, 2007). There is seasonality in the concentration of foliar nutrients, with the difference between deciduous and evergreen species decreasing continuously throughout the rainy season. Deciduous species compensate the shorter time of energy return from their leaves (lower range of leaf length) through investment in leaves with higher assimilation potential. This justifies the greater leaf nutrient concentrations and a predominance of metabolic compounds over the structural construction of leaves, as indicated by the SLA (Franco et al., 2005).

2.3. Disturbances – fire and deforestation

Fire is a factor of recognized ecological importance in the Cerrado, influencing the nutrient cycling and affecting the dynamics of the vegetation, particularly the grass/woody biomass ratio. Paleoecological studies recorded the presence of particles of charcoal in the region 18,000 years BP (Salgado-Labouriau and Vicentini, 1994) indicating the occurrence of fire before the presence of humans. In the last few decades, fire events have become more frequent with cerrado stricto sensu being burned every 2-3 years while open areas such as campo sujo and *campo limpo* might be burned annually (Coutinho, 1990).

Fire leads to mortality of woody plants, exposes the soil to erosion and consumes the litter and herbaceous layer causing the release of nutrients and a temporary increase in their availability (Miranda and Bustamante, 2002 for a review). Consequently, there is a redistribution of nutrients accumulated in the woody layer as well as in the litter layer (Haridasan, 2001). In a fire event, the nutrients can be volatilized, lost in the transport of particles, deposited as ash or remain in the unburned vegetation (Kauffman et al., 1994). If fires are followed by rain events, leaching of nutrients to deeper soil layer can occur (Resende et al., 2010). As fire frequency increases, the grass-tree ratio tends to increase (Sato et al., 1998), and the vegetation physiognomy shifts to a more open form, which subsequently favors the occurrence of intense fires (Miranda et al., 1996). Greater losses of C, N and S of the aboveground biomass pools have been observed after fires from grassland formations than from cerrado *sensu stricto* and cerrado (Kauffman et al., 1994). The differences in nutrient stocks and the higher fuel consumption during fires in more open areas of Cerrado may explain the lower nutrient losses with greater density of woody plants. The woody components of the vegetation are the major pool of nutrients, and generally do not burn during surface fires. Additionally, the nutrient stock in the leaves of the woody plants is smaller than the nutrient contained in the

live biomass of the herbaceous layer (see Miranda and Bustamante, 2002 for a review).

By the year 2004, remnants of native Cerrado vegetation covered less than 50% of the original area of the domain and only 2.2% of this area was under legal protection (Klink and Machado, 2005). An estimate based on data for 2002 indicated that the main land use activities were pasture and croplands, covering respectively about 27% and 11% of the Cerrado area (Sano et al., 2010). Additionally, it should be considered that cattle ranching also occupies part of the natural grasslands (about 23 million ha).

The carbon and nutrient dynamics are basically modulated by the biota, especially through photosynthesis as one of the major links between atmosphere and terrestrial ecosystems. To fully understand the biogeochemical cycles and how they affect the functioning of the system and are affected by changes in vegetation cover, it is essential to quantify fluxes and stocks and evaluate their main environmental drivers and controls. In the next sections, we will present some data available for native and managed ecosystems in the Cerrado.

3. Carbon Cycling

3.1. Above and belowground carbon stocks

The understanding of changes in vegetation biomass (above and below ground) and the soil organic matter pools in different Cerrado physiognomies is essential to estimate emissions of greenhouse gases from deforestation. According to the Brazilian Greenhouse Gases Inventory (Brasil, 2010) the carbon emissions due to deforestation in the Cerrado increased from 0.05 Pg C yr⁻¹ (1988 to 1994) to 0.06 Pg C yr⁻¹ (2002 to 2008).

The structural diversity of Cerrado vegetation types involves a range of total biomass. The total biomass (sum of above and below ground measured up to 2 m depth) in the Central Brazil ranged from 21.8 Mg ha⁻¹ in the *campo sujo* to 77.8 Mg ha⁻¹ in the *cerrado denso*. Regarding root/shoot ratio, all physiognomies showed values higher than 1, ranging from 2.6 in the *cerrado aberto* to 7.7 in the *campo limpo* (Castro and Kauffman, 1998). Similarly, Lilienfein et al. (2001) estimated a total above and belowground biomass of 22.7 Mg ha⁻¹ and 30.4 Mg ha⁻¹, respectively, in other cerrado *sensu stricto* area. Forestlands present high aboveground biomass. Delitti and Burger (2000) reported a total aboveground biomass of about 136 Mg ha⁻¹ for a gallery forest located in the southern Cerrado region. Although these data indicate the importance of belowground biomass, soil organic matter is the most important stock of carbon in Cerrado ecosystems. Abdala (1993) estimated carbon stocks in different compartments of a typical cerrado area. Considering the vegetation and soil up to 1-m depth, the total carbon stock was 265 Mg ha⁻¹, and 70% of this amount was composed of soil organic matter (185 Mg ha⁻¹).

Soil microbial biomass usually represents only about 3% of soil carbon stocks (Silva and Mendonça, 2007).

However, it is a carbon compartment with a very high turnover rate compared to other soil carbon forms and is strongly influenced by land use. Rainfall seasonality affected the soil microbial biomass in two native vegetation types (cerrado *sensu stricto* and *campo sujo*) protected from fire, with values ranging from 162.2 to 929.3 mg C kg soil⁻¹, affecting also the soil community structure (Viana, 2002) and diversity (Silva, 2004).

3.2. Litterfall and litter decomposition

Annual flux of fine litter in Cerrado areas ranges from 210 (cerrado *sensu stricto*) to 780 g m⁻² yr⁻¹ (cerradão) (Peres et al., 1983; Silva, 1983, 2004; Nardoto et al., 2006) with leaf litter accounting for more than 75% of total litterfall (Nardoto et al., 2006). Litter production is markedly seasonal with the highest litterfall, particularly of leaf fraction, occurring at the end of the dry season (August – September) (Nardoto et al., 2006). This rate is similar to values found in other seasonal ecosystems but is lower than those found in terra-firme forests in the Amazon (700 to 1000 g m⁻² yr⁻¹) (Cuevas, 2001; Bustamante et al., 2004a).

In a typical cerrado, fine litter decomposition rates indicate a litter turnover time range from 1.1 to 9.9 years (Peres et al., 1983; Silva, 1983; Constantino, 1988; Resende, 2001; Cianciaruso et al., 2006; Valenti et al., 2008). The Cerrado litter residence time is higher than the global mean steady state litter turnover that usually ranges from 1.4 – 3.4 years (Matthews, 1997). Decomposition studies in typical cerrado areas have indicated accumulation of mass and nutrient litter, especially in areas protected against fire (Oliveira-Júnior, 1985; Resende, 2001).

3.3. Impacts of disturbances and management on carbon stocks and fluxes

The stock of litter in the Cerrado is dependent on fire frequency (Constantino, 1988; Resende, 2001). Constantino (1988) reported values between 3 Mg ha⁻¹ and 5.3 Mg ha⁻¹ while Resende (2001) found 5.6 Mg ha⁻¹ in areas subjected to fire events and 13.3 Mg ha⁻¹ in areas protected from fire. The dead standing herbaceous layer is a usually underestimated component of litter. In typical cerrado areas the dead standing herbaceous achieved 4.7 Mg ha⁻¹ (Meirelles and Henriques, 1992). The reduction by 22% in the fine litter production one year after fire (Nardoto et al., 2006) can be related to the higher mortality rates of woody species after successive fire events (Sato and Miranda, 1996; Sato et al., 1998). The reduction of litterfall from woody species resulted in nutrient fluxes 60 - 80% lower in the burned area than in the unburned area (Nardoto et al., 2006). Besides the reduction of the woody layer, differences in species susceptibility to fire (Mistry, 1998) may have consequences for nutrient cycling. On the other hand, frequent burnings seem to not affect the structure of soil microbial communities in spite of differences in the soil water content and pH between burned and unburned plots (Viana, 2002; Silva, 2004).

Soil carbon stocks in soils are not strongly affected by burning events. Roscoe et al. (2000) compared three

typical cerrado areas with a different incidence of fire occurrences. Soil carbon stocks did not differ significantly and values were about 195 Mg ha⁻¹ (up to 1 m depth). Compared to the C stocks in the biomass, soils represent more conservative stocks in response to fires.

Long term use for pasture and cropland can either promote soil organic matter losses or gains. Soil carbon loss in consequence of management occurs mainly in the surface soil layer (0 – 20 cm depth). Carbon stocks in this soil layer under native Cerrado vegetation were estimated at approximately 50 Mg ha⁻¹ (Bustamante et al., 2006a). Maia et al. (2009) studied the pastures in northwestern Cerrado areas and observed that reformed pastures show carbon sequestration rates in soil ranging between 0.61 and 0.72 Mg ha⁻¹ yr⁻¹, in contrast to degraded pastures that had reducing rates at 0.28 Mg ha⁻¹ yr⁻¹. The recovery of degraded pastures has implications for C sequestration as well as for the conservation of native Cerrado areas considering the large area of pastures in the Cerrado region currently showing traits of degradation (Peron and Evangelista, 2004). Change in land use (pasture compared with native areas) affected also the density and abundance of soil microorganisms (Viana, 2002) with pasture areas presenting lower diversity (Quirino et al., 2009).

In croplands, the use of sustainable management systems has been considered to mitigate greenhouse gases emissions, and prevent environmental degradation. The rate of carbon accumulation in soils under no-tillage compared with conventional tillage systems in the Cerrado region ranged between 0.3 and 1.91 Mg C ha⁻¹ yr⁻¹ (Batlle-Bayer et al., 2010). Another management system suggested is the crop-livestock integration, which combines crops, especially soybeans and grasses. This system tends to optimize the management practices when associated with reduced fertilization and tillage (or no-till), increasing animal production and reducing soil degradation. However, its potential to carbon sequestration compared with continuous grazing systems can still be considered limited and requires further studies (Marchão et al., 2009).

3.4. Soil CO₂ emissions

Soil CO₂ flux is an important component of the system that is strongly influenced by temperature and humidity (Pinto et al., 2002). These two environmental variables were determinants for the seasonality of soil CO₂ fluxes in a typical cerrado and in a dense cerrado with higher values during the rainy season than in the dry season (Pinto et al., 2002; Aduan, 2003; Pinto, 2003). The annual soil CO₂ fluxes in native areas ranged from 12 Mg C ha⁻¹ yr⁻¹ to ~15 Mg C ha⁻¹ yr⁻¹ (Aduan, 2003; Pinto, 2003). The onset of the rainy season increased the CO₂ flux and artificial water addition in a *campo sujo* during the dry season significantly increased the CO₂ flux by almost 5 times. However, the effect was short-lived (three days after addition) (Pinto et al., 2002).

Comparing soil respiration in different Cerrado physiognomies, Pinto et al. (2002), found that after successive fires, burned areas showed higher CO₂ emissions

in the wet season than unburned areas, indicating the long term effects of burning. Successive burning promotes tree mortality and increases grass cover, and consequently increases the contribution of root activity in soil respiration. Shortly after the conversion of native vegetation to pasture, soil respiration also increases (Pinto et al., 2006).

3.5. Net ecosystem exchange

Grace et al. (2006) made an estimate for tropical savannas, including the Cerrado, of an uptake of 0.14 Mg C ha⁻¹ yr⁻¹, contributing to a total sink of 0.39 Gt C yr⁻¹, almost 15% of all C fixed by world vegetation. Determinations of seasonal CO₂ fluxes using Eddy covariance showed that a typical cerrado in Central Brazil (vegetation had been burned by fire of low intensity seven years before the experiment) was a CO₂ sink during the rainy season and source during a brief period at the end of dry season (Miranda et al., 1996, 1997). The annual balance indicated a net uptake of about 2.5 Mg C ha⁻¹ yr⁻¹ (Miranda et al., 1996). In another study, Rocha et al. (2002) also showed a net C uptake in a typical cerrado area but to a lower extent (0.1 to 0.3 Mg C ha⁻¹ yr⁻¹). These differences could be related to heterogeneity of vegetation in different areas and physiognomies. Working in a woodland cerrado area at the transition between Amazon and Cerrado Domains, Vourlitis et al. (2001) emphasized that seasonal variations in rainfall have important implications for the seasonal pattern of net ecosystem CO₂ exchange.

4. Nitrogen Cycling

4.1. Atmospheric deposition of nutrients and biological nitrogen fixation

In general, Cerrado ecosystems are N limited systems and the rates of N cycling differs according to the density of woody plant, fire frequency, land use changes, N deposition and N fixation (see Bustamante et al., 2006b for a review). Atmospheric deposition of total N in a typical cerrado area in Central Brazil was ~4.0 kg ha⁻¹ yr⁻¹, with a half of this being inorganic N (Resende, 2001). This value of total atmospheric deposition is 3.4% of the stock of N in litter and less than 0.1% of total soil N (000-100 cm). Resende (2001) further determined that the amount of N leached from the canopy and accumulated in the litter is about 5.1 kg N ha⁻¹ yr⁻¹, and that the canopy leachate is enriched with organic N.

Biological nitrogen fixation (BNF) might represent an important flux of N from the atmosphere to the biota. Global estimates for terrestrial ecosystems indicated that around 128 Tg N yr⁻¹ enter via BNF, providing approximately 15% of N supply over all types of biomes (Galloway et al., 2004). Also according to this estimate, about 70% of BNF would occur in regions with warmer climates - Africa (25.9 Tg N yr⁻¹), Latin America (26.5 Tg N yr⁻¹) and Asia (21.4 Tg N yr⁻¹). The BNF in tropical savannas was estimated at 16-44 kg N ha⁻¹ yr⁻¹ and was considered as the main source of N in these systems (Cleveland et al., 1999).

Fabaceae is the most abundant family in the Cerrado, but direct data on BNF in natural systems are scarce. The natural abundance of heavy isotope of nitrogen (^{15}N), expressed as $\delta^{15}\text{N}$ in ‰, is a tool for assessing long-term fixation (Ehleringer and Rundel, 1989). Species that are not capable of fixing atmospheric N_2 show a wide variation in their isotopic ratio depending on the rate of N mineralization in soil. For the Cerrado, in general, Bustamante et al. (2004b) and Nardoto (2005) showed that, on average, legumes have lower values of $\delta^{15}\text{N}$ and higher concentrations of leaf nitrogen (more than 1%) than non-legumes. It seems that most legumes, particularly those of Faboideae are active fixers of N under natural conditions. However, for a more accurate assessment of the contribution of legumes to the N balance in Cerrado it is necessary to understand the controls on the density of legumes and seasonal variation of the BNF.

4.2. Nitrogen mineralization

As stated before, the decomposition rates in typical cerrado areas are relatively low. The average loss of biomass was 32% after one year and immobilization of N, P and S was observed (Resende, 2001). Regarding N mineralization, Nardoto and Bustamante (2003) found in a typical cerrado protected from fire in Central Brazil that the amount of available inorganic N was $14.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, while an area subjected to frequent fire was only $3.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The rates of net N mineralization increased during the rainy season when there was a reduction in soil microbial biomass in plots both burned and protected from fire. This suggests a pattern of a peak of microbial activity with the onset of the rainy season and initial N immobilization followed by net mineralization. In the Cerrado, despite the increase in net rates of N mineralization and nitrification during the rainy season, the concentrations of inorganic-N decreased during the rainy season, indicating the effect of plant uptake. The low rates of nitrification in a typical cerrado area with consequent predominance of $\text{NH}_4\text{-N}$ in soil (Nardoto and Bustamante, 2003) are typical of more conservative systems with cycles of N (Davidson et al., 2001). This, together with the high C/N ratios of litter (~60/1), contribute to the low rates of decomposition and mineralization of organic matter in the Cerrado, thus maintaining the low availability of N in this system.

4.3. Emissions of N oxides

Soil emission of N gases (NO and N_2O) from soils under native Cerrado vegetation are very low (Pinto et al., 2002). Cerrado areas protected from fire emitted via NO soil fluxes between 0.1 and $0.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ while annual emissions from burned areas were around $0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. However, estimates of annual soil emission of NO are complex due to occurrence of short-lived pulses that increase variability. Pinto et al. (2002) observed that water addition to dry soils increases NO soil fluxes by a factor of 10. Similarly, fire events resulted in emissions of NO , two times higher than before fire fluxes, but the effect disappeared after five days. Thus, pulses of emissions

must not add more than 10-20% of the estimated annual emissions. N_2O fluxes were below the detected limit of the equipment for Cerrado soils.

5. Phosphorus Cycling

While the atmosphere is an important source of N and C, phosphorus is mainly derived from the weathering of primary minerals (Schlesinger, 1997). In the long term, soils have their mineral reserves depleted, reaching a terminal and irreversible condition of absence of nutrients derived from rocks (Chadwick et al., 1999). High weathered Oxisols predominant in the Cerrado region (Reatto et al., 1998) present high P chemical adsorption and low P availability (Mesquita Filho and Torrent, 1993).

In Cerrado areas of Central Brazil P flux through bulk precipitation ranged from 0.01 to $0.94 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (Coutinho, 1979; Lilienfein and Wilcke, 2004; Parron et al., 2010; Resende et al., 2010). Variability of P in bulk precipitation might result from ash deposition by local fire events (Coutinho, 1979) but usually low concentrations of P in bulk precipitation result in lower fluxes by atmospheric deposition (Lilienfein and Wilcke, 2004; Resende et al., 2010). The few data on watershed budgets in the Cerrado region indicated a closed system, with low input by atmospheric deposition ($0.01 \text{ kg ha}^{-1} \text{ yr}^{-1}$), throughfall ($0.008 \text{ kg ha}^{-1} \text{ yr}^{-1}$), litter leachate ($0.006 \text{ kg ha}^{-1} \text{ yr}^{-1}$) and low output by stream water ($0.001 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Resende et al., 2010).

Soil P content, irrespective of fraction, was higher in Cerrado soils in the uppermost soil layers (Resende et al., 2010). The determinant of P availability was the soil internal biogeochemical cycle. Due to the weathering processes, occluded P forms are the dominant form in Cerrado Oxisols (Lilienfein et al., 2000; Resende et al., 2010). In this terminal steady state, the P availability is determined by organic fraction dynamics (Johnson et al., 2003), especially by microbial biomass P dynamics (Resende et al., 2010). While available P (Mehlich I) was less than 1 kg ha^{-1} in 0-50 cm depth, P in microbial biomass was 27.9 kg ha^{-1} in the wet season and 14.3 kg ha^{-1} in the dry season. The magnitude of microbial P is better understood when compared with plant biomass P ($27.1 \text{ kg P ha}^{-1}$) (Resende et al., 2010).

Microbial soil populations are key components of the soil-plant continuum affecting plant development. P-solubilizing microorganisms can solubilize and mineralize P from inorganic and organic pools of total soil P (Oliveira et al., 2009). Under severe environmental conditions, which restrict plant occupation, such as soil scarcity and nutrient deficiency, inoculation with mycorrhizal fungi increased leaf P concentrations in cerrado plants used in restoration of degraded areas (Matias et al., 2009). In soils under natural cerrado vegetation the role of soil microbiota in P cycle needs further studies. Faunal activity may alter soil P fractions and soil availability in Cerrado areas. Termite activity resulted in a gross enrichment of labile P forms in the termite nest in Cerrado (Rückamp et al., 2010).

The litterfall-P flux in the Cerrado was also low (0.4 kg P ha⁻¹ yr⁻¹ in the fine litter) partly as a result of high P resorption rates (Nardoto et al., 2006). The litter P stock determined in woodland cerrado was 4.6 kg ha⁻¹ and the C/P ratio was 1,300 (Resende, 2001) indicating limitation to microbial decomposition activity (C/P > 200 described in Paul and Clark, 1989). Immobilization of P during decomposition was observed with residence time of P in litter of 8.7 yr⁻¹ contrasting with litter residence of 2.9 yr⁻¹. Fire events reduced litterfall (Nardoto et al., 2006) and litter stock from 13.3 Mg ha⁻¹ to 5.6 Mg ha⁻¹ (Resende, 2001) consequently reducing litter P stock to 4.6 to 2.0 kg ha⁻¹ (Resende et al., 2010). Besides, repeated burning decreases the organic-P fraction and P availability in Cerrado soils at 0-10 cm. Another effect of fire in the Cerrado was an increase in P concentration of soil solutions at 100 cm depth, indicating a pathway for P loss (Resende et al., 2010).

6. Interactions Between Nutrients

Variations in leaf $\delta^{15}\text{N}$ would reflect different mechanisms to sustain a great diversity of species in nutrient-poor and seasonally water-stressed ecosystems. However, despite the variation of about 10‰ in $\delta^{15}\text{N}$ leaf found in Cerrado areas of Central Brazil (Bustamante et al., 2004b; Nardoto, 2005; Coletta et al., 2009) values are less enriched in ^{15}N when compared with those of species of upland forests of the Amazon (Nardoto et al., 2008). Bustamante et al. (2004b) attribute the large variability in the plants of the Cerrado $\delta^{15}\text{N}$ to factors such as mycorrhizal associations, large variation in soil depth and a seasonal change in the processes of immobilization and net N mineralization in these soils. There were significant and positive correlations between the $\delta^{15}\text{N}$ leaf with leaf N concentration, as well as foliar concentration of P (Nardoto, 2005).

In the case of a typical cerrado area, nutrient use efficiency at community level is about 4373 for P and 137 for N (Nardoto et al., 2006) suggesting that cerrado vegetation is more limited by P than by N. However, N limitation is higher in the Cerrado than in tropical rain forests (Nardoto et al., 2008).

At species level, the nutrient concentrations in fresh leaves are lower than those in other tropical woody species and do not show large variation among different phenological types (deciduous, brevi-deciduous and evergreen) (Nardoto et al., 2006). In general, nutrient concentration is more closely related to a particular trait (e.g. legume species with high N demand or Al-accumulating species). Leaf N concentration varies more than P concentration, but as the soil P availability is very low (Resende et al., 2010), P in leaves of the cerrado species is already at minimal levels, which leads to a narrow range of concentrations. Aerts and Chapin (2000) define values of N/P < 16 as N limitation, values 14 < N/P < 16 as co-limitation by N and P and value of N/P > 16 as P limitation. In an area of typical cerrado in Central Brazil, the average N/P ratio in green leaves for ten woody species was 18, indicating that

N supply is low, but also a greater limitation by P than by N (Nardoto et al., 2006).

Some elements such as N, P, K and S can readily move from leaf to leaf, whereas others such as Fe and Ca are relatively immobile once they reach leaves (Taiz and Zeiger, 1991). For the cerrado woody species the mean retranslocation efficiency ranges from 14.5 to 37.2% for N and from 40 to 70.4% for P (Nardoto et al., 2006). In this context, cerrado woody plants seem to be more dependent on resorption efficiency for the P supply than for the N supply.

In a typical cerrado area the immediate effects of burning result in a temporary increase in concentrations of Ca, Mg, K and N at the soil surface (0-5 cm) but P concentration did not change (Batmanian and Haridasan, 1985). On the other hand, P concentration increased in one species but decreased in two other species in the burned plot. Batmanian and Haridasan (1985) observed, for the ground-layer community of a typical cerrado, that the concentration of all nutrients in the aerial biomass was generally higher in the burned area during the first year after the fire. The temporary enrichment of nutrients in the soil after the burning may result in higher nutrient concentrations in leaves, but the ability of woody plants to use this available pool depends on the timing of resprouting. Susceptibility to fire is a consequence of different plant characteristics such as bark thickness, height, diameter, plant architecture, chemical composition and ability to resprout (Mistry, 1998) and apparently is not directly correlated to leaf phenology and ecophysiological responses to nutrient availability. However, changes in the community structure due to frequent fires may have strong impacts on nutrient cycling and regeneration of vegetation cover through the amount and quality of litterfall that are dependent on species responses.

The stocks of available K, Ca and Mg in a typical cerrado area are larger in total biomass than in soil (Table 1). This pattern is consistent with the description of poor soils with low cation exchange capacity as the Cerrado Oxisols, which are not able to retain large amounts of cations (Resende, 2001). In this case, atmospheric deposition may be an important source of available nutrients as primary minerals are absent in matrix rock. The input of nutrients through atmospheric deposition in Cerrado systems was representative with respect to the stocks of Ca, Mg and K in the soil. Fire events may cause an impoverishment of these nutrients in Cerrado ecosystems by reducing litterfall, litter stock and plant biomass.

7. Impacts of Nutrient Addition on the Processes of Nutrient Cycling in a Typical Cerrado

The proximity of natural and urban areas, the continuous addition of nutrients due to the intensification of agricultural activities (Tilman et al., 2002) and the changes of fire regimes at the global level (Bowman et al., 2009) contribute to increasing inputs of nutrients in natural ecosystems. If

Table 1. Stocks of nutrient in shoot and root biomass, litter and soil in a typical cerrado on clayey Haplustox (Latossolo Vermelho Escuro) (adapted from Resende, 2001).

Component stock	Biomass	N	P	K	Ca	Mg	S
	kg ha ⁻¹						
Aboveground biomass ^a	37,787	NA	12.6	81.0	62.8	30.1	NA
Litter	13,308	123	4.6	10.5	46.9	12.8	8.2
Belowground biomass ^b	27,649	103	8.8	54.9	66.9	19.2	13.2
Total biomass	74,744	226	26.0	146.4	176.6	62.1	21.4
Soil ^c	-	4,576	2,042	81	77	25	nd

^aThe estimate of plant shoot nutrients was determined by Silva (1990) considering tree density estimated by Nardoto (2000) and the herbaceous stratum estimate by Batmanian (1983). NA means not available. ^bNutrient root stock up to 8-meters depth. ^cSoil nutrient stock up to 1-m depth.

is estimated that the average atmospheric deposition of N in the world's 34 biodiversity hotspots in the year 2050 will double the average rate of atmospheric deposition observed in all terrestrial ecosystems during the 1990s (Phoenix et al., 2006).

An experimental addition of nutrients was initiated in 1998 in a typical cerrado area in Central Brazil showed that the total annual litter production in the treatment with N addition was higher in the second year of fertilization (Kozovits et al., 2007). It was observed that even with the increased availability of N, P and K in the soil, specific leaf area of different woody species was not altered. Fertilization altered the processes of nutrient cycling, stimulating increases of soil microbial biomass and accelerating the rate of litter decomposition. The addition of nutrients also resulted in the alteration of water regulation by woody plants (Scholz et al., 2007).

Nine years after the beginning of the experiment and after the occurrence of an accidental fire in 2005, the effects of combined application of N and P were more intense than the individual effects of adding these elements, suggesting that the Cerrado could be co-limited and/or the addition of an isolated element exacerbate the limitation by another (Jacobson et al., 2010). Simultaneous addition of N and P affected density, dominance, richness and diversity patterns more significantly than addition of N or P separately. Leaf litter decomposition rates increased in P and NP plots but did not differ in N plots in comparison to control plots. The results indicate that if the availability of P is not increased proportionally to the availability of N, the losses of N are intensified. It seems that there are positive interactions between the addition of nutrients and vegetation responses to fire, increasing the resilience of the ecosystem. This result was observed through the positive effect of adding N and NP on the recovery of leaf litter production in the post-fire period in comparison to the production in the pre-fire period.

Responses of the herbaceous layer to nutrient additions, floristic diversity was significantly different between the treatments. The highest and lowest species richness was presented in control and NP, respectively. The addition of P alone or in combination with N induced invasion by *Melinis minutiflora* (exotic C₄ grass). The aboveground

biomass of this species was higher in NP and P plots. In the N treatment *Echinolea inflexa* (native C₃ grass) presented elevated cover and biomass but *M. minutiflora* was absent. The invasion by alien species (*M. minutiflora*) resulted in negative impacts on native grass species. Besides changes in aboveground biomass, addition of N and P also led, although to a lesser extent, to changes in the root morphology and biomass, but these responses were modulated by seasonal variation in soil moisture (Bustamante et al., 2012).

8. Interactions Between Terrestrial and Aquatic Systems

Gallery forests of the Cerrado Domain play a critical role in controlling stream chemistry but little information is available about biogeochemical processes in these forest formation. Parron et al. (2010) described the fluxes of N and P in solutions along a topographic gradient in a gallery forest. Three distinct floristic communities were identified along the gradient: a wet community nearest the stream, an upland dry community adjacent to the woodland savanna and an intermediate community between the two. The lower fluxes via soil solution and stream water in comparison to other flowpaths emphasize the conservative nutrient cycling of these forests and the importance of internal recycling processes for the maintenance and conservation of riparian and stream ecosystems in the Cerrado.

Primary productivity in small streams is mostly originated from input of leaf litter from riparian vegetation. A study that evaluated the decomposition rate of different leaf residues and the dynamics of nutrient release in different seasons in a small stream in a well-protected gallery forest showed that the rate of litter decomposition is strongly influenced by the quality of the detritus and the main characteristics related with decomposition are concentrations of secondary compounds, carbon and C:N ratio. The rate of decomposition and nutrient release were more intense during the wet-dry season than in dry-wet season due to changes in the hydrological and chemical characteristics of the stream. Decomposition is faster in the aquatic systems than in the terrestrial ecosystems of the Cerrado. Comparison of N fluxes suggests that part

of N released could be retained in sediment or released by denitrification (Mitre, 2011).

Biogeochemical evaluations of the impacts of land use changes in the Cerrado region are still scarce in spite of its hydrological importance on a country-wide scale. Land use changes in the Cerrado, often coupled to increased fire frequency and invasion of exotic species, result in changes in the vegetation structure and functioning of these ecosystems.

In general, these changes in land use are first reflected in the biogeochemistry of small streams (Richey et al., 1997), which are important biogeochemical elements in landscapes as they connect the terrestrial environment with large rivers, and their chemistry is affected by biotic and abiotic processes such as climate, hydrology, soil properties, geomorphology, topography and land use (Thomas et al., 2004). Silva et al. (2010) evaluated streams that drain areas under natural, rural, and urban land cover in the Cerrado central region. Chemical concentrations generally followed the pattern of Urban > Rural > Natural. Stream water conductivity in urban streams was three and five-fold greater in relation to rural and natural areas, respectively. In the wet season, despite increasing discharge, concentration of many solutes was higher, particularly in rural and natural streams. Streams also presented higher total dissolved N (TDN) loads from natural to rural and urban although DIN:DON ratios did not differ significantly. In natural and urban streams TDN was 80 and 77% dissolved organic N, respectively. These results indicate that alterations in land cover from natural to rural and urban are changing stream water chemistry in the Cerrado with increasing solute concentrations and declining organic N dominance with potential effects on ecosystem function.

Floodplains are ecosystems that generally feature a principal river whose waters periodically go beyond the fluvial channel to flood the adjacent areas during a determined time period (Junk et al., 1989). The periodic cycles of flood, known as flood pulses, are the principal driving forces responsible for several environmental and biological alterations in these ecosystems, controlling the development and maintenance of biodiversity.

One of the most important Brazilian floodplains is that of the Araguaia River, located in the Cerrado Domain, in the Center-West region. The Araguaia sub-basin, which is part of the Tocantins-Araguaia Basin, has a drainage area of approximately 386,478 km², entirely located within Brazil. It is 2,110 km long and can be divided into three units: High, Medium and Low Araguaia (Latrubesse and Stevaux, 2002). It is submitted to a total average annual precipitation is 1,751 mm and the river's average discharge is 5,508 m³ s⁻¹ (Aquino et al., 2005).

In spite of the well-known ecological, economic and social importance of the Araguaia River floodplain, the interest of the scientific community in this region remained low and static until recently, but has gradually increased since 2006 (Vieira, 2008). Even classical limnological hypotheses, such as the seasonal variation of environmental

parameters in floodplains, are still insufficiently evaluated in the Araguaia basin.

Among those few studies, Vieira (2008) evaluated the effect of the flood pulse on total phosphorous and nitrogen concentrations (which are the main limiting variables of aquatic primary production) in the pelagic zone of 22 lakes in the Medium Araguaia River Basin. The two sampling campaigns were conducted in the rainy season (January of 2006; mean monthly discharge = 2,551 m³ s⁻¹; mean monthly precipitation = 293 mm) and dry season (July of 2006; mean monthly discharge = 519 m³ s⁻¹; mean monthly precipitation = 5 mm). As expected, the concentrations of those variables was higher during the rainy season, featuring about 56 and 49% more total phosphorous and nitrogen, respectively, in the lakes.

Therefore, understanding the real relationships between the seasonal variations of water levels and the physical-chemical compositions in floodplains constitutes the basis for understanding the spatial and temporal structure of their biological communities. Besides, this understanding results in a central theoretical framework in the development of conservation strategies in these environments.

9. Potential Impacts of Climate Change on the Functioning of Cerrado Ecosystems

Different regional climate models often result in different predictions of climate change. Marengo et al. (2009) produced regional projections of temperature and rainfall for South America with three regional climate models. Although such models produce predictions with some differences, it is possible to highlight aspects of agreement among the models and additionally to list the predictions of less and more severe changes expected for each study region. These models considered the expected changes in temperature and precipitation in the Cerrado for the year 2100 using the IPCC A2 scenario (IPCC, 2000). This scenario simulates the concentration of greenhouse gases in the atmosphere if a relatively high population growth (approximately 15 billion people in 2100) is maintained, in a heterogeneous world in terms of availability and use of resources, in which regions with the highest abundance did not prioritize increased resource use efficiency. Under this scenario, the development of alternative sources of energy would be slow, resulting in a dominance of fossil fuels during the whole period.

The more severe predictions for temperature change indicated that most of the Cerrado would experience an increase of about 4 °C, except for the areas in the transition with the Amazon (Tocantins and Maranhão states) where an increase of 6 °C is expected. The less severe predictions indicated an increase of 2 °C in the eastern part of the Cerrado and of 4 °C in the other areas.

Regarding precipitation, the projection of more severe changes indicates a decrease of 20 to 50% of current values of precipitation in the central and southern parts of the Cerrado, and reductions of about 70% in the northeastern part. The projections with less severe changes indicate a

reduction of 30% in the central and southern parts of the Cerrado and a reduction of 50% in the northeastern area.

Changes in the distribution of rainfall throughout the year in the Brazilian Cerrado are also expected (Marengo et al., 2010). In the north-northeast of the Cerrado, an increase of 20 to 30 days in the length of the dry season (maximum number of consecutive days without rain) is expected. Similarly, a decrease in the number of rainy days per year is expected in Tocantins, northern Goiás, northeastern Mato Grosso and the central region of Minas Gerais. On the other hand, an increase in the volume of rainfall coming from storms is expected in central-southern Cerrado.

The overlap of the expected climate changes for the Cerrado and distribution of the main centers of biodiversity in the Cerrado (*sensu* Castro, 1994), indicates that the diversity center of the Northeastern Cerrado will be more severely affected. A study including data on 162 tree species of the Cerrado predicted that 39 ~ 48% of these species would be extinct depending on different climate change scenarios (Siqueira and Peterson, 2003). Considering the total number of species, thousands of species would then be at risk. Over the past 40 years the vegetation in the Cerrado has rapidly been transformed and fragmented due to agricultural expansion (Sano et al., 2008). The study also indicated that the area of distribution of the selected tree species will be restricted to the southern part of the Cerrado. This is the region of the Cerrado with massive land conversion. It is unlikely that Cerrado plant species may suffer dispersion through a matrix of agricultural areas to reach natural areas with more favorable climates. Thus, the combined effects of climate change, habitat loss and little representation in the national system of protected areas can be catastrophic. Climate modeling results illustrate the complexity of predicting future patterns of precipitation and the heterogeneity of climate system responses across the Cerrado region (Bombardi and Carvalho, 2008). Such aspects associated with the pattern of distribution of biodiversity in the Cerrado (high alpha and beta diversity) indicate the need for monitoring systems that consider the different conditions in the sub-regions of the Cerrado.

A schematic representation of the main plant functional groups in the Cerrado and the expected changes related to climate change is presented in Figure 1. The balance between woody (trees/shrubs) and herbaceous vegetation is an important aspect of Cerrado physiognomies. These two groups of plants have different characteristics not only in the use of resources and resistance to disturbance, but also have different roles in the cycling of elements. Trees and shrubs provide more recalcitrant stocks of nutrients in the form of deep roots and stems, while the herbaceous vegetation is more readily decomposed or consumed by fire (Miranda and Bustamante, 2002). Thus, the expectation of increased representation of herbaceous vegetation caused by an intensified fire regime in areas where an increase in the length of the dry season is expected, would represent a less conservative cycling of elements.

Despite the strong seasonality of rainfall in the Cerrado, and the consequent low availability of water in upper

soil layers, less than 5% of the species in the region are herbaceous annuals (Miranda and Bustamante, 2002). However, in an area of northeastern Cerrado subject to an aridization process, an atypical balance between annual and perennial herbs was observed, with approximately 30 annual individuals for each perennial individual (Filgueiras, 1991). This change in life strategy predominantly associated with soil degradation, shows that there are thresholds of nutrient availability and drought severity that favors perennial or annual life forms. The impoverishment of soils associated with the intensification of fires and increase in the length of the dry season could therefore favor annual species.

Functional aspects of the herbaceous vegetation of the Cerrado may also change in response to the temperature rise expected in the Cerrado, in particular the abundance of plants with C_3 and C_4 metabolism. The balance between C_3 and C_4 grass is related to temperature and CO_2 concentration. Warmer environments favor the richness and productivity of C_4 species (Hattersley, 1983) while higher ambient concentrations of CO_2 tend to favor the productivity of C_3 species (Collatz et al., 1998). In studies evaluating

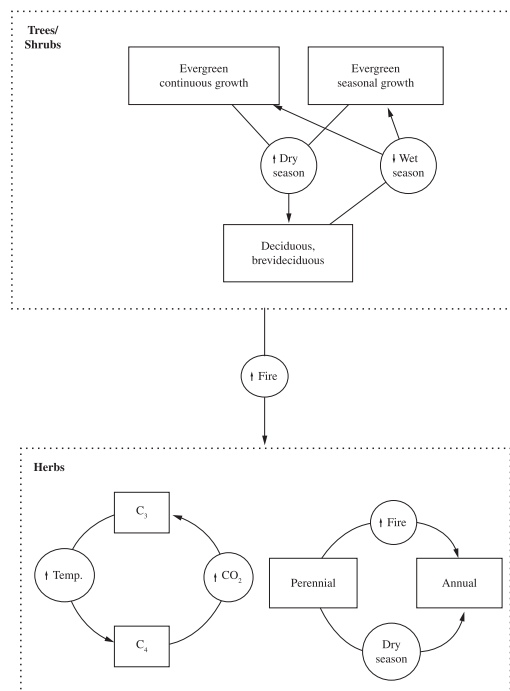


Figure 1. A diagrammatic representation of the major plant functional groups in the Cerrado ecosystems and the expected changes in the balance of these groups related to climate change (predicted for the year 2100 by Marengo et al., 2009). Boxes indicate vegetation groups (dashed lines) or sub-groups (solid lines). Arrows represent the direction of the balance change among vegetation groups. In the circles are indicated the driver of change: increase in the length of the dry season; reduction of precipitation in the wet season; increase in the fire events; increase in the temperature; increase in the CO_2 atmospheric concentration.

the isotopic composition of carbon in soil organic matter in the grasslands in Mongolia and North America there is evidence of the preponderance of the effect of temperature in regulating the productivity of C3 and C4 plants (Wittmer et al., 2010). However, it is difficult to predict the precise result of this balance, since the interactions of temperature and CO₂ concentration were not considered in the projections for the next century. Changes in the balance between C₃ and C₄ plants can additionally represent changes in the abundance of species in association with microorganisms capable of nitrogen fixation due the legume richness found in the Cerrado herbaceous layer. Currently, the grasses are herbaceous plants with a large coverage area in the Cerrado. In a *campo sujo*, Munhoz and Felfili (2006) estimated that 67% of the area was covered by grasses while legumes covered only 3.9%. Whereas most species of grasses in the Cerrado region have C4 metabolism (Klink and Joly, 1989), the projected increase of atmospheric CO₂ concentration could favor plants with C3 metabolism, like legumes.

The decrease in rainfall and increase in dry season length could potentially alter the balance between woody plants with different phenological strategies. Under this scenario, evergreen species could be impaired if water availability in soils during the dry season became insufficient to maintain the leaves, considering that many evergreen species of Cerrado have shallow roots, with depths up to 100 cm (Goldstein et al., 2008). Brevi-deciduous and deciduous species could also present negative effects under these conditions. As stated in a previous section, an important difference between deciduous/brevi-deciduous and evergreen species is that the period of leaf payback of the first group is shorter as their leaves have a shorter life span (less than a year). In order to achieve a positive carbon balance between carbon assimilation and leaf production cost, deciduous plants tend to have higher photosynthetic rates and leaves with lower production costs (higher SLA) (Franco et al., 2005). In a scenario with longer and more intense droughts the period of payback for deciduous/brevi-deciduous species would be even shorter. This aspect, in association with a reduction in photosynthetic rates expected in an environment with lower water availability, may result in a negative carbon balance.

Another important characteristic of deciduous, brevi-deciduous and evergreen species with seasonal growth is the concentration of leaf production in the dry season (Lenza, 2005). Working in an African savanna, Archibald and Scholes (2007) observed that the length of day is the main factor that triggers the onset of leaf production. Thus, in plants with this environmental trigger, leaf production is dissociated from soil water availability and the leaves can be produced before the onset of the rainy season. In the Cerrado region, the adjustment between the photoperiod as an environmental signal for the proximity of the rainy season will be mismatched by the predicted increase of dry season length. Lenza (2005) suggested that the decrease in temperature at the beginning of the dry season may represent a signal for leaf abscission in deciduous and brevi-deciduous species even with high water availability

in the soil. Additionally, this author raised the possibility that leaf production in all phenological groups could be triggered by the increase in atmospheric evaporative demand and decrease of water content in soil. If such factors are the main environmental triggers for the phenological events, it can be assumed that plant phenology would respond directly to climate changes in temperature and rainfall.

The scarce data on leaf dynamics and phenology and the relatively restricted geographic distribution of the studies impair more accurate forecasts of possible changes in the balance of different phenological groups. Information regarding the ability of savanna species to acclimate to different rainfall conditions by processes such as regulation of stomatal conductance and change in total leaf area of the individuals is essential for improving predictions. In addition to new field studies the use of remote sensing techniques could help to define regional differences in leaf shedding and leaf production events and to improve the evaluation of climate variables that can act as environmental triggers of these phenological events.

Primary productivity of the Cerrado will potentially suffer a reduction in the light of projected changes in climate. Despite the increased photosynthetic efficiency due to higher atmospheric CO₂ concentration, changes in water availability and increases in temperature will likely result in a greater inhibitory effect (Bonan, 2008). The temperature rise will result in the reduction of photosynthetic efficiency, related to decreased affinity of the enzyme Rubisco for CO₂ and the increase of evaporative demand (Berry and Björkman, 1980) The rise in evaporative demand would result in less available water for vegetation and increased water loss through evapotranspiration. Thus, the stomatal regulation of transpiration would be more conservative, resulting in decreased photosynthetic rates. Additionally, increased length of the dry season, projected to occur in the northern and northeastern savanna, would result in a longer period of the year when the Cerrado functions as source of C to the atmosphere. All these factors thus indicate a decrease in the annual net primary productivity of the Cerrado.

The increase of the length of the dry season could potentially result in increased vulnerability to fires. Fires in the Cerrado, including those caused by human activities, typically occur during the dry season, being more common in the middle and late season (Mistry, 1998). Additionally, fires with greater flame intensity occur primarily in the middle of the season, when most of the combustible material is dry. Thus, increasing the duration of the dry season expected to occur in the north-northeastern of the Cerrado may represent an increased likelihood of fires and increased impact of these events. More frequent and intense fires could result in smaller stocks of biomass and nutrients in the litter and increased loss of nutrients from the system through leaching, erosion, transport of particles and volatilization. Under this scenario, soils have an important role in the conservation of C in the system.

In the case of reduction of primary productivity across the Cerrado, CO₂ emissions would tend to diminish due to

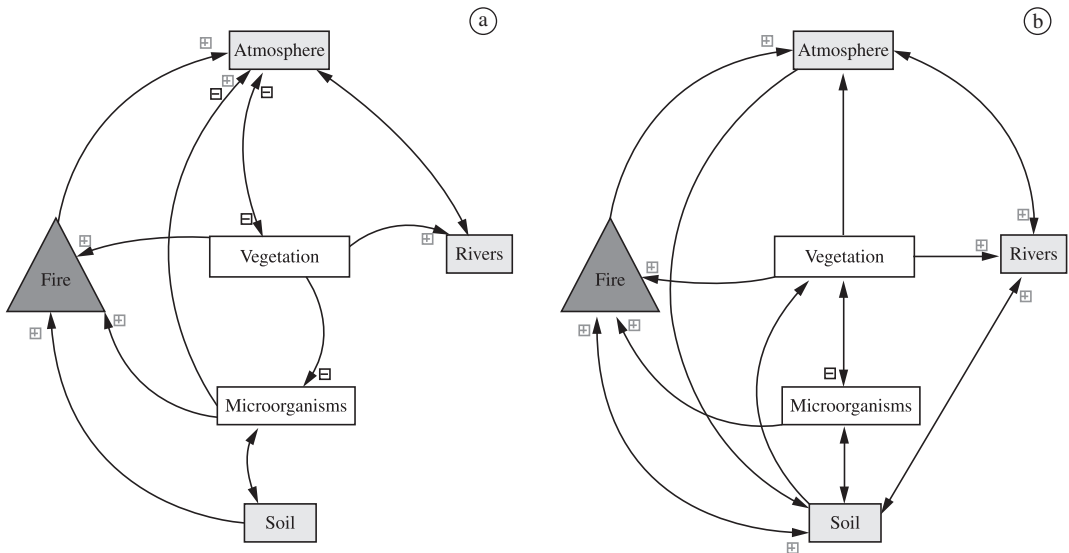


Figure 2. Schematic representation of the main compartments (boxes) and fluxes (arrows) of a) carbon and b) nitrogen in the Cerrado and the expected changes related to climate change (predicted for the year 2100 by Marengo et al., 2009). *White boxes* are biotic compartments, *shaded boxes* abiotic compartments, and *triangles* are changes mediated by fire. *Small boxes with plus or minus sign* indicate increase or decrease for a given flux.

the reduction of litter production, microbial activity and lower metabolic rates of the roots. Additionally, since the emission of CO₂ from the soil tends to decrease during the dry season in the Cerrado (Pinto et al., 2002), a potential increase in the length of the dry season in the northeastern region of this domain could result in a further decrease of annual values. The possible increased frequency of fires in this region could also influence CO₂ emissions from the soil as Cerrado areas subject to repeated fires have higher CO₂ emissions during the rainy season (Pinto et al., 2002).

Biogeochemical cycles in the Cerrado, as stated in previous sections, are regulated by the seasonal distribution of rainfall. The cycling of P and N are particularly dependent on the biomass and activity of microorganisms. Studies on the diversity and structure of microbial communities pointed out that these aspects differ significantly between the rainy and dry seasons. If these changes will be heightened by changes in climate and how this will impact the cycling of nutrients demands further studies.

The increase in rainfall volume resulting from storms that is projected to occur in the south-central portion of the Cerrado might result in increased leaching of nutrients. Thus, in addition to the degradation of riparian vegetation, such as gallery forests, due to land use changes, a decreased in the ability to retain nutrients in terrestrial environments and a transient increase in their concentration in aquatic systems through more intense storms is expected.

While on global and regional scales the distribution of savannas is controlled by climate, particularly by the amount of precipitation and seasonality, on finer scales the biogeochemical characteristics and history of disturbances, particularly the fire regime, become determinants of structure and functioning of these ecosystems. The results of studies

on nutrient cycling from long-term experiments in Cerrado areas showed that this vegetation is co-limited by N and P availability and that changes in N and P cycling has a direct impact on the biodiversity of the Cerrado.

Climate models predict changes in temperature, amount and distribution of precipitation that vary according to different Cerrado sub-regions. This, in addition to the heterogeneity in the composition and abundance of biological communities across the Cerrado Domain and to the interactions with land use changes, makes projections of impacts of future climate scenarios very complex. Moreover, current climate models are not considering the interactions of vegetation responses to climate with responses to other variables such as increasing CO₂ atmospheric concentration and N deposition. A schematic representation of the expected changes on the fluxes of carbon and nitrogen is presented in Figure 2. The intensification of fires due to changes in climate might cause a reduction in the woody vegetation and litter layer affecting fluxes and stocks of nutrients. N and P cycling are particularly dependent on microbial processes and the impacts of climate change on the microbiota are poorly understood. The projected climate change might also have impacts on the functioning of Cerrado ecosystems decreasing C uptake. However, in spite of the increasing number of studies focusing on the interactions between carbon and nutrient cycling in Cerrado ecosystems, these studies are concentrated on the central part of the domain. The understanding of potential impacts of climate change demands more information on spatial and temporal variability of terrestrial and aquatic ecosystems and new modeling approaches that consider the feedback from different environmental stressors.

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