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Nitrogen cycling in tropical and temperate savannas

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Abstract. Savannas are the most common vegetation type in the tropics and subtropics, ranging in physiognomy from grasslands with scattered woody plants to woodlands with heterogeneous grass cover. Productivity and organic matter turnover in savannas are controlled by interactions between water and nutrient availability, and this basic environmental structure is modified by fire frequency and land management practices. We compared temperate and tropical savannas in order to understand the strength of nitrogen (N) limitation of productivity. American tropical and temperate savannas are N limited systems, and the N cycle differs according to the woody plant density, fire frequency, land use change, N deposition and N fixation. Grazing and conversion to pasture have been the predominant land-use changes in most savannas. In the Cerrado and the Llanos tropical savannas, intensified use of fire for pasture management is leading to decreased woody plant density. Oppositely, in the Chaco and North American temperate savannas, fire suppression and grazing are leading to increases in woody density. In addition, the higher soil P availability in the Gran Chaco and the higher N deposition in North American savannas may be contributing to increases of N cycling and net productivity rates. Some aspects of the N budget for savannas of the American continent are still unclear and require further analysis to determine rates of N fixation, and to understand how spatial and temporal soil heterogeneity control N fluxes through soil solution and into streams.

Introduction

Savannas are the most common vegetation type in the tropics and subtropics (Solbrig 1991; Scholes and Archer 1997). They cover extensive areas of South America, Africa and Australia, and also occur in Central America, India, and North America (Figure 1). In a broad sense, savannas can be defined as ecosystems with a near continuous grass/herbaceous stratum, a discontinuous layer of trees and shrubs of variable density, and where growth patterns are closely associated with alternating wet and dry seasons (Bourlière and Hadley 1983 in Mistry 2000). The dry season can last from 2 to 9 months, and there is also substantial climate variability between years (Frost et al. 1986).

Savanna ecosystems are controlled by the interactions between water and nutrient availability, as savanna vegetation often occurs either on weathered

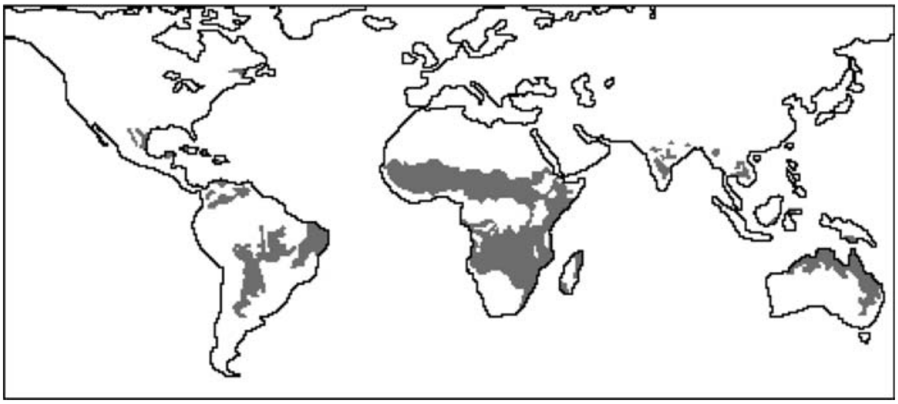


Figure 1. The approximate global distribution of tropical grasslands, savannas and woodlands (derived from Olson et al. (1983) by Scholes and Hall (1996).

soils with low nutrient availability, in regions of limited rainfall, or both (Medina 1987; Sarmiento 1996; Reatto et al. 1998). This basic environmental structure is modified by additional factors such as fire frequency and land management practices. Almost one fifth of the world's population lives in savanna regions (Frost et al. 1986), and these are probably the oldest ecosystems used by people, as they have supported hunting and pastoral practices for millennia. Presently savannas are experiencing many transformations due to agricultural intensification, over-grazing and changes in fire regimes. However, there is little understanding of the strength of N limitation of productivity, especially when comparing temperate and tropical savannas. This understanding requires data on inputs, outputs and internal cycling. Medina (1993) presented an extensive review of the mineral nutrition in tropical savannas containing considerable information concerning the N cycling. In this paper, we present a comparison between temperate and tropical American savannas based on the inputs, outputs and internal cycling of nitrogen. The interactions between N and other elements controlling the N cycle, as well as the effects of disturbance and land use changes, are presented.

In South America, savannas occur in two large patches north and south of the Equator (Solbrig 1996). The principal tropical savanna region south of the equator occurs entirely within Brazil, mostly in the central region of the country, is locally known as the Cerrado and covers approximately 2 millions km^2. This wet seasonal savanna is a mosaic of plant formations with a gradient of woody plant density ranging from open grasslands (campo limpo) through open scrubland (campo sujo and cerrado *sensu stricto*) to dense woodlands (cerradão) (Eiten 1972). The tropical savannas of northern South America (the Orinoco Llanos) extend from the Guaviare river in Colombia to the eastern coast of Venezuela covering approximately 500,000 km^2 (Sarmiento 1983). Vegetation physiognomy can also vary widely across the Llanos: from tree-less savanna grasslands to savanna woodlands with up to 80% tree cover (Sarmiento 1984).

In the subtropical region of South America, there are different ecosystems dominated by grasses, generally with sparse trees that can be considered as savannas due to the structure and function, but most of them differ remarkably from tropical savannas (Sarmiento 1996). Flooding and fire are key environmental factors that may differ, and drought is associated with low temperatures during the winter. While dystrophic acid soils dominate in the tropical savannas, soils are mesotrophic in the subtropical systems, and alkalinity and salinity can be important edaphic factors. These subtropical savannas reach a higher diversity in the Gran Chaco region in Bolivia, Paraguay, Argentina and small areas in Brazil. They are complex vegetation mosaics that vary throughout the Chaco region.

In North America, sub-tropical savannas dominated by the genera *Prosopis* (mesquite), *Acacia* and *Andropogon* are found throughout much of Texas and northern Mexico, or more than 500,000 km^2 (Bailey 1996). Areas of North American savannas are now dominated by introduced grasses of African origin (D'Antonio and Vitousek 1992; Asner et al. 2004). These savannas support a wide range of vegetation physiognomies, from open grasslands with sparse trees to dense mesquite woodlands having a nearly continuous understory of herbaceous cover. Rainfall in the sub-tropical savannas of North America, Australia and Africa ranges from less 400 mm to more than 1200 mm, and mean annual temperatures vary from 9 to 27 °C. Soils also vary substantially from oxic Ultisols on exposed Permian surfaces throughout Northern Texas to sandy alluvial Inceptisols in Northern Mexico and Arizona (SCS 1962).

In large regions of North and South American and Australian savannas, the vegetation has been heavily impacted by overgrazing following the introduction of large-scale cattle management practices (Asner et al. 2004). For example, in the Argentine Chaco region, grasslands disappeared and were replaced by a dense and thorny shrubland following years of heavy grazing (Morello and Saraiva-Toledo 1959; Bucher and Schofield 1981). In the Cerrado region, Indians and farmers used fire for the past several thousand years. The analysis of a sediment core of 6000 years revealed the presence of charcoal particles in all depths, indicating the occurrence of burning throughout this period (Vicentini 1999). However, in recent times the use of fire has become much more intensive with the conversion of extensive areas of Cerrado to pastures and grasslands. In other areas, fire suppression along with overgrazing and climate change are implicated in a widely observed shift from open savanna grasslands to ecosystems now densely populated by trees and shrubs (Archer 1995). In Texas grasslands and savannas, encroaching mesquite (*Prosopis glandulosa* var. glandulosa) has caused an increase in above-ground biomass, which, in turn, has increased soil carbon (C) and nitrogen (N) storage (Hibbard et al. 2001; Asner et al. 2003; Asner and Martin 2004).

Because global savannas cover an area of about 19.3 million km^2 and are typically burned at a frequency of 5 years or faster, they are important for regional and global atmospheric chemistry (Crutzen and Andreae 1999). The nitrogen cycle is particularly sensitive to changes induced by frequent fires due to substantial loss of this element through volatilization. In addition to the impacts of frequent fires on the N cycle, recent increases in anthropogenic deposition of N in natural ecosystems are more pronounced in grasslands and savannas (Asner et al. 2001). These authors pointed out that the primary controls over the fate of N in such regions are likely to be quite different than in forested systems, which have been the traditional focus of N pollution studies. The quantification of inputs and outputs of N in savanna ecosystems demands a more intensive research effort, as scarce information is available on N fixation rates and on both gaseous and solution N losses.

N inputs, outputs and internal cycling

Fire-nitrogen interactions

Nitrogen fluxes in savanna ecosystems are strongly influenced by the fire regime to which they are subjected. This is true of all savannas, independent of their geographical location (e.g., tropical or temperate). Fire affects the dynamics of the vegetation, particularly the grass/woody biomass ratio (Scholes and Archer 1997). Surface fires, which consume the fine fuel of the herbaceous layer, are the most common in savannas but fine fuel load varies with the degree of woodiness. The fine fuel of the herbaceous layer ranged from 85 to 97% of the fuel load from woodland savannas to open savannas in Central Brazil (Miranda et al. 2003). 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 savannas and cerradão woodlands (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 they do not burn during surface fires. Additionally, the nutrient stock in the leaves of the woody plants (Silva 1990) is smaller than the nutrient contained in the live biomass of the herbaceous layer (Batmanian 1983).

Nitrogen loss occurs through volatilization and via particulate matter formation during combustion and during subsequent wind-born transport (Kauffmann et al. 1994). Pivello and Coutinho (1992) estimated that, during a cycle of six prescribed fires in a *campo sujo* area (grass-dominated vegetation type), about 95% of the nitrogen in plant biomass was released to the atmosphere. In addition to the losses of nitrogen through biomass burning, several authors have shown that fire increased soil emissions of NO and N_2O

(Ward et al. 1992; Neff et al. 1995; Weitz et al. 1998; Wahlen et al. 2000). The emissions of N oxides in savannas are discussed further in Section 'Emissions of NO and N_2O' (below).

Atmospheric deposition

A study conducted in a cerrado area protected from fire in Central Brazil estimated total N input from atmospheric deposition at 4.2 kg ha^{-1} yr^{-1}, with a contribution of 2.2 kg ha^{-1} yr^{-1} as inorganic N (Resende 2001). This value of total atmospheric deposition corresponds to 3.4% of the litter stock but to less than 0.1% of the total N in the soil (0–100 cm). The same author determined that the N leached from the canopy and accumulated litter amounted to 5.1 kg N ha^{-1} yr^{-1}. Canopy and litter leachate was enriched in organic N.

A similar value of 2.2 kg ha^{-1} yr^{-1} was reported for the input of inorganic N from bulk precipitation and dry deposition in a *Trachypogon* savanna in Venezuelan Llanos (Montes and San Jose 1989). The input of NH_4-N was 2.0 kg ha^{-1} yr^{-1}, but organic nitrogen input was not measured. The reported inputs of inorganic N in the South American savannas are lower than the values found in an African savanna (~5 kg ha^{-1} yr^{-1}) (Villecourt and Roose 1978 cited by Abbadie et al. 1992). Comparing atmospheric deposition inputs and the amount of N in above- and below-ground plant biomass in a *Trachypogon* savanna, Montes and San Jose (1989) suggested that 19.5% of the N required for maximum biomass of 482 g m^{-2} during growth season was supplied by atmospheric deposition. They pointed out that the distribution of rains seemed to determine essential differences in the nutrient inputs, as the ratio of the nutrient input during the rainy and the dry season ranged from 2.3 to 7.8. Unusual differences in dry deposition chemistry between years seemed to be related to length of the dry season, occurrence of sporadic rains during the dry season, and the quality and quantity of fuel material. However, it cannot be assumed that all atmospheric deposition would be readily available for plant uptake. A recent report from Pacheco et al. (2004) for the Llanos indicated that soluble organic N inputs may be an important contribution, making up 80% of the total soluble N in rainfall. It remains to be established if this soluble organic N constitutes a net N input to the soil–vegetation system.

Nitrogen deposition has been monitored in temperate and sub-tropical savannas of Texas, USA as part of a national monitoring network (NADP 2003). NO_3 deposition varies from 6 to 10 kg N ha^{-1} yr^{-1}, depending upon geographic location, local and regional wind and rainfall patterns, and land use. Deposition of NH_4 ranges from 2 to 4 kg N ha^{-1} yr^{-1}, resulting in a total wet deposition range of about 8–14 kg N ha^{-1} yr^{-1}. These values are considered high, as they rival values observed in areas of the northeastern USA thought to be undergoing N pollution and saturation (Asner et al. 2001).

Nitrogen fixation

Global biological N fixation (BNF) in terrestrial ecosystems has been estimated at 128 Tg N yr^{-1}, supplying ~15% of the N requirement across all biome types (Galloway et al. 2004). According to this estimate, about 70% of BNF occurs 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}). Cleveland et al. (1999) compared global patterns of N fixation in natural ecosystems, and they included Cerrado vegetation in the xeromorphic woodlands category with BNF values of 9–34 kg N ha^{-1} yr^{-1}. The same study presented the N-fixation in tropical and wet savannas ranging from 16 to 44 kg N ha^{-1} yr^{-1}, concluding that this process is the major source of N in these systems.

An early attempt to estimate nitrogen balance in the savannas of northern South America was published by Medina (1982). This review concluded that N losses caused by burning grassland biomass amounted to less than 1% of the total soil N inventory down to 30 cm depth. However, the preliminary balance was strongly negative without including inputs through BNF. A more recent attempt to balance the N budget for the Orinoco savannas was published by Sanhueza and Crutzen (1998). In their budget (summarized in Table 1), the most uncertain numbers are those of N input via biological fixation, particularly in nodulated legumes. Without improved BNF values, as well as output data such as NH_3 volatilization, the calculated N balance ranges from −1.7 to −11.1 kg N ha^{-1} yr^{-1}. These values are small considering that Orinoco savannas contain between 4000 and 5000 kg N ha^{-1} (Medina 1982). However, until the uncertainties in the biological N fluxes are clarified, the ecological significance of these losses on ecosystem function in the long-term remains unclear.

Data on stocks and fluxes of N in a typical cerrado area (approx. 50% woody cover) protected from fire for 28 years compiled from several studies carried out on the same system are shown in Table 2. The total stock of N in the area is 1357 kg ha^{-1} considering the N stocks in soil (= 1116 kg N ha^{-1} in the 0–10 cm depth – this layer is supposed to be more influenced by the 28 years of fire suppression), in the biomass of green leaves of woody species (= 24 kg ha^{-1} – most of the N is allocated in leaves for photosynthesis), in the belowground biomass (= 95 kg ha^{-1} – roots 2 mm in 0–100 cm depth) and in fine litter (= 123 kg ha^{-1}). The inputs range from 20 to 48 kg ha^{-1} yr^{-1} considering 4 kg ha^{-1} yr^{-1} through atmospheric deposition and 16–44 kg ha^{-1} yr^{-1} through N fixation. The outputs in the absence of fire are very low as the N_2O emissions are negligible and NO emissions represent a loss of only 0.4 kg ha^{-1} yr^{-1}. Although data on N fluxes in streams are not yet available, they might also be negligible, as concentrations of NH_4+ and NO_3- in cerrado streams are 5–10 times lower than in streams of the eastern Amazon (Markewitz et al. 2001; Parron 2004). At an input rate of 20–48 kg ha^{-1} yr^{-1}, the time to accumulate a stock of 1357 kg ha^{-1} ranges from 28 to 68 years, which encompasses the time of fire suppression in the area (~28 years).

Table 1. General nitrogen budget for the Orinoco savannas (modified from Sanhueza and Crutzen 1998).

Process	Flux (kg N ha^{-1} yr^{-1})
N fixation	
Blue-green algae	1–2
Azospirillum associations	1.3–8
Nodulated legumes	(10–20) (estimated)
Atmospheric deposition	
Wet deposition	
NO_3	0.65–1.3
NH_4	0.56–3.3
Dry deposition	
$NO_2 + NO_3 + HNO_3$	0.42–0.87
$NH_4 + NH_3$	4.1–9.7
Total input	8–26 (9–46) considering estimated legume contribution
Denitrification	
N_2O	0.18–0.63
N_2	0.36–6.3
Biomass burning	
NO_x	1.2–3.6
NH_3	0.75–2.3
N_2O	0.05–0.15
RCN	0.35–1.1
N_2	6.5–20
NO emissions from soils	0.3–3
NH_3 volatilization	(5.5–8.5) (estimated)
Total output	9.7–37.1 (20–45.3) considering NH_3 volatilization

In temperate savannas of North America, estimates of biological N fixation range from 5 to 35 kg ha^{-1} yr^{-1} (Rundell et al. 1982). With higher N deposition (8–14 kg ha^{-1} yr^{-1}), the total inputs are estimated at 13–49 kg ha^{-1} yr^{-1} (Table 3). In comparison to outputs via N oxide trace gas emissions (0.3–3.4 kg ha^{-1} yr^{-1}; Martin et al. 2003) and low biomass burning fluxes due to widespread fire suppression (Archer 1995), the inputs are enormous and likely decreasing the strength of nitrogen limitation of primary production in many regions. For example, Asner and Martin (2004) used field and published data to show that total plant N requirement for a Texas savanna was about 21 kg N ha^{-1} yr^{-1} on oxic Ultisols with low woody and herbaceous plant cover, well within the range of estimates of N input via deposition and biological fixation. While woody encroachment in these regions increases the demand for nitrogen, soil organic N and N mineralization rates increased significantly, which suggests that N fixation increases with woody encroachment to accommodate N demand (Table 3). At this time, biomass burning

Table 2. General nitrogen budget for a cerrado *sensu stricto* protected from fire for 28 years.

Compartments	Stock (kg ha^{-1})	References
Total N – soil (0–100 cm)	4576	Resende (2001)
Total N – soil (0–10 cm)	1116	Resende (2001)
Aboveground biomass (woody species)	37,787	Silva (1990)
Belowground biomass (0–800 cm) (roots >2 mm)	27,649	Klink et al. (unpublished data)
Belowground biomass (0–100 cm) (roots >2 mm)	25,638	Klink et al. (unpublished data)
Fine litter production (kg ha^{-1} yr^{-1})	2300	Nardoto et al. (2006)
N in the biomass of leaves of woody species	24	Considering that leaves represent 5% of total aboveground biomass (Silva 1990) and that the mean N concentration in the leaves is 12.5 g kg^{-1} (Nardoto 2006)
N in the belowground biomass (0–800 cm) (roots >2 mm)	103	Resende (2001)
N in the belowground biomass (0–100 cm) (roots >2 mm)	95	Resende (2001)
N in the fine litter	123	
Process	Flux (kg ha^{-1} yr^{-1})	
Internal cycling		Nardoto and Bustamante (2003)
N mineralization (0–5 cm)	14	
N fixation	16–44	Cleveland et al. (1999)
Atmospheric deposition (wet + dry deposition)	4	Resende (2001)
Total input	20–48	
NO emissions from soils	0.4	Pinto (2003)

estimates of N losses or redistribution are scarce because fire suppression has been much more common throughout many temperate savannas (Scholes and Archer 1997).

N_2-fixation by Legume–Rhizobia associations

A characteristic feature of South American savannas is the high diversity of herbaceous and woody leguminous species. In fact, many of the forage legume species cultivated today in the tropical world originate from South America (Winter et al. 1989). Most legumes in tropical savannas live in association with native *Rhizobia* strains. In a large survey of legume species of the savannas in Venezuela, Barrios and Gonzalez (1971) found 109 nodulated species out of a total of 127 species investigated. Most of the nodulated species were within the subfamily Papilionoidae (73 species). The frequency of legume species in Venezuelan savannas has been associated with low levels of exchangeable Al and high levels of exchangeable Ca (these two parameters are inversely correlated; Medina and Bilbao 1991). In natural savannas, legumes have leaf

Table 3. General nitrogen budget for temperate mesquite savannas of North America.

Compartment	Stock (kg N ha^{-1}) without woody encroachment	With woody encroachment	References
Soil organic N	1900 on clays	3200 on clays	Asner and Martin (2004)
(0–30 cm)	2700 on loams	3100 on loams	
Process	Flux (kg N ha^{-1} yr^{-1})		
Internal N cycling N	16.2 (9.6) on clays	29.6 (8.2) on clays	Asner and Martin (2004)
mineralization	117.6 (19.7) on loams	167.5 (26.9) on loams	
(0–30 cm)	60 (1)	140 (30)–220 (20)	Hibbard et al. (2001)
N fixation			
Legumes	5–35		Rundell et al. (1982)
Atmospheric deposition			
Wet deposition			
NO_3	6–10		NADP (2002)
NH_4	2–4		NADP (2002)
Total input	13–49		
N_2O emissions from soils	<0.5	<0.5	Martin et al. (2003)
NO emissions	0.3 (0.2) on clays	0.6 (0.2) on clays	Martin et al. (2003)
from soils	2.4 (0.4) on loams	3.4 (0.5) on loams	

nitrogen concentrations above the critical level for normal growth; however, the levels of P and of K are clearly deficient. This nutrient status may lead to a decrease in plant growth due to the inhibition of effective nodulation (Medina and Bilbao 1991). Although the density and diversity of legume species in Cerrado areas are high (Felfili et al. 1992), there are very few reports about the activity of nodules in legume species occurring in this region (Leitão 1997). Low nodule activity was measured in Cerrado legume species of southeast Brazil (Faria et al. 1984), while another series of studies stressed the nodulation deficiency of the species with such capabilities (Campelo 1976; Döbereiner and Campelo 1977; Magalhães et al. 1982). Besides the need for N fixation by the plant, the magnitude of nodulation depends on the density of bacteria populations, and on the physical and chemical properties of soil. Factors such as P and Ca limitation, high soil acidity, Al saturation, and seasonal water stress may constrain BNF in tropical savannas of the Llanos and Cerrado. In the Chaco, Mazzarino et al. (1991a, b) worked with the dominant tree species *Prosopis flexuosa* DC (Fabaceae) and *Aspidosperma quebracho-blanco* Schlecht (Apocinaceae), and pointed out that N availability in soil under the legume species is higher than under the non-legume species as a consequence of the legume capacity to biologically fix nitrogen.

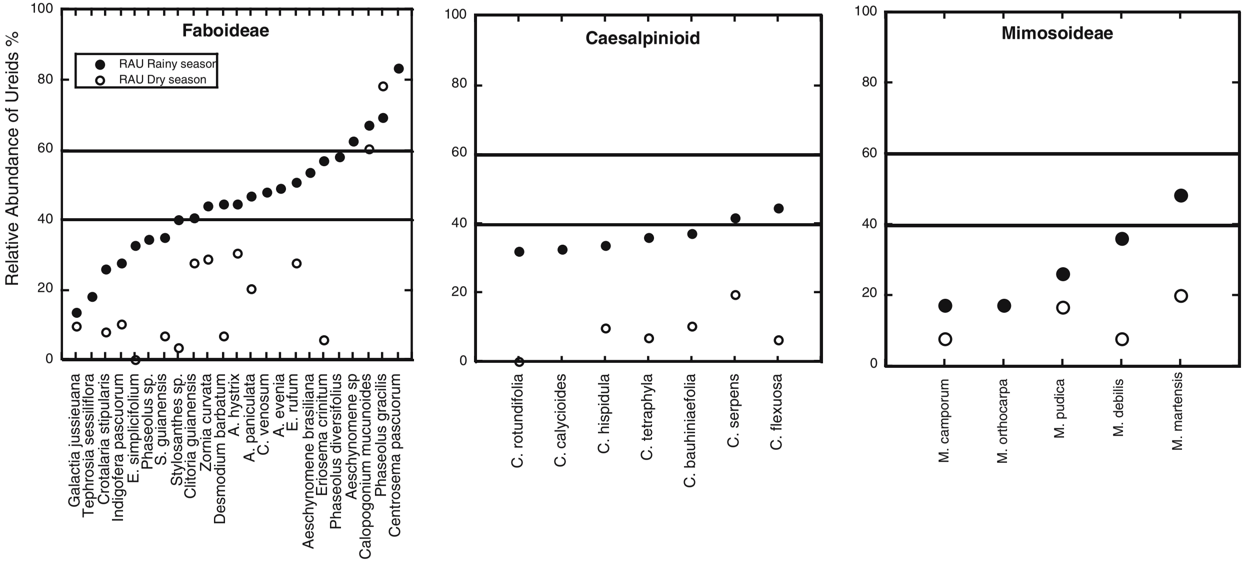
Very little is known about the spatial and temporal dynamics of BNF in North American savannas. The geographic extent of the major leguminous genera (e.g., *Prosopis*, *Acacia*) have been determined by Johnson and Mayeux (1990) who observed a large percentage of surveyed *Prosopis glandulosa* plants with nodules, with maximum occurrences in southern Texas and New Mexico.

Rates of BNF have been estimated in *Prosopis*, *Acacia* and other genera in Southern Texas (Zitzer et al. 1996; Archer et al. 2001). Based on Zitzer et al. (1996), we estimate BNF rates of up to 25 kg N ha^{-1} yr^{-1}. However, they emphasized that substantial variations are caused by water availability and the degree of woody cluster development, both of which affect soil N accumulation rates and total stocks. Rundell et al. (1982) estimated BNF among *Prosopis* plants at about 6–35 kg N ha^{-1} yr^{-1}. Like tropical systems, estimates of the temporal and spatial variability of BNF must be improved if the N balance of temperate savannas is to be understood.

Despite the few studies directly documenting nitrogen fixation by native legumes under natural conditions in South American savannas, there is some indirect evidence suggesting N fixation for a few species. These indirect evidences are based on the natural abundance of ^{15}N and the concentration of ureids and α-amino compounds in the xylem sap of young shoots (Medina and Bilbao 1991; Izaguirre-Mayoral et al. 1992; Sicardi de Mayorca and Izaguirre-Mayoral 1993).

The relative abundance of ureid (RAU%) was used by Izaguirre-Mayoral et al. (1992) as an index for nitrogen fixation capacity of herbaceous and suffrutescent legume species in central Venezuela. This index is based on the assumption that ureids are the form in which fixed nitrogen is exported from the nodules in the majority of tropical legumes. Soluble nitrogen compounds are extracted with alcohol from young stems and the total N content and its distribution in inorganic-N, α-amino-N and ureid-N is determined. RAU values above 60% are recorded in species with high nitrogen fixation activity, while values below 40% are indicative of low N_2 fixation activity. In Figure 2, the results of Sicardi de Mayorca and Izaguirre-Mayoral (1993) have been drawn to show the differences in N_2-fixation capacity in species separated in subfamilies, and measured during the peak of the rainy and dry seasons. The Faboideae contains most of the species studied. Besides, the best N_2-fixers are also within this subfamily. Drought strongly affects N_2-fixation capacity, as expressed by the reduction in RAU.

RAU values indicate short term N_2-fixation activity. To evaluate long-term fixation, the use of the natural abundance of ^{15}N, expressed as δ^{150}N in , appears to be the method of choice. The rationale is that within the same environmental conditions, N_2-fixing species have more negative values than non-fixing species. A few papers have reported large variations in δ^{15}N in species of South American savannas (Medina and Bilbao 1991; Sprent et al. 1996; Bustamante et al. 2004a; Medina and Izaguirre 2004). These papers show that, on average, the legumes have lower δ^{15}N (1–4) and higher N concentrations (~1%) than non-legumes. However, trees are consistently more negative than shrubs, irrespective of plant family (Bustamante et al. 2004a). Soils both in central Brazilian Cerrados and central Venezuelan savannas have strong positive δ^{15}N values (>3), and for the Venezuelan data set (Medina and Izaguirre 2004), the plant–soil difference of δ^{15}N values ranges from −4 to −6 for legumes and −0.4 to −2.1 for non-legumes. The Brazilian study



Arrangement of legumes species according to subfamily and Nitrogen Fixation Capacity (NFC)
measured by the Relative SAbundance of Ureids (RAU%)
(Modified from Sicardi de Mallorca and Izaguirre-Mayoral 1993)

NFC	RAU %
HIGH	>60
INTERMEDIATE	40-60
LOW	<40

Figure 2. Arrangement of legumes species according to subfamily and NFC measured by the RAU% (modified from Sicardi de Mallorca and Izaguirre-Mayoral 1993).

(Bustamante et al. 2004a) reports strongly positive soil $\delta^{15}N$ values (>10) at depths of 1–2 m. It seems clear that most legumes, particularly those of the subfamily Faboideae, are active N_2-fixers under natural conditions but to have a reliable assessment of the contribution of legumes to the N budget of savannas it is necessary to understand controls over legume density and seasonal nitrogen fixation activity.

N_2-fixation by free-living microorganisms

Cyanobacteria can make important contributions to soil N in most humid savannas. In the *Trachypogon*-savannas of Central Venezuela, with 10–12% cyanobacterial coverage, N_2-fixation rates during the rainy season varied between 0.4 and 0.7 mg N m^{-2} day^{-1} (Santaella 1985). According to Chacón et al. (1991), these N-fixation rates would be enough to compensate potential N losses that can occur through fire.

Free-living bacteria in the rhizosphere of grass roots have been reported to fix significant amounts of atmospheric nitrogen (Boddey and Döbereiner 1995). The reports are somewhat inconsistent, and disagreement persists regarding the significance of this activity for the nitrogen budget of natural savannas. van Berkum and Day (1980) reported rates ranging from 14.7 to 51.4 g N ha^{-1} day^{-1} in field grown Brazilian grasses. It seems more likely that rhizospheric nitrogen fixation can occur as a slow but continuous process contributing small amounts of organic nitrogen to savanna ecosystems. These amounts, however, could become significant in areas where plant productivity is severely limited by nitrogen availability (Giller and Day 1985) or where legumes are not numerous (Abbadie et al. 1992). Nonsymbiotic nitrogen fixation has been reported to be a significant contribution to the nitrogen budget in savannas from West African. For these savannas, Robertson and Rosswall (1986) have reported N fixation from free-living bacteria of about 12 kg ha^{-1} yr^{-1}. Abril and Bucher (1999) also concluded that nitrogen fixation by free-living microorganisms is an important process in the Chaco, particularly in degraded areas. They measured changes in soil characteristics, nutrient availability and microbial activity in a gradient of grazing intensity (highly restored, moderately restored and highly degraded). Nitrogen fixation was more intense at the moderately restored site (no grazing for 8 years), followed by the highly degraded site (overgrazing), with the lowest values at the highly restored site (no grazing for 20 years). The authors suggested that high nutrient availability (particularly phosphorous) in the Chaco allows BNF (by both free-living and symbiotic organisms) and organic matter production to shape vegetation structure and function, including response to over-grazing. The Western Chaco soil nutrient contents are relatively high when compared to other savannas of the world (Table 4), most of which are located in highly weathered soils of much older origin (Huntley and Walker 1982). Effects of P limitation on BNF are discussed further in this paper. Additionally, the comparison of soil properties of the different savannas indicates that soil organic N is also relatively

Table 4. Comparison of organic carbon content, soil total nitrogen, C/N ratio and available in different savanna regions.

Ecosystem	Organic carbon %	Total nitrogen %	C/N	Extractable P (μg g^{-1})	References
Chaco (restored site)	4.7	0.28	16.8	52.5	Abril and Bucher (1999)
Llanos	1.2	0.07	17.1	2.3	Medina (1982)
Brazilian Cerrado	3.2	0.17	18.8	0.2	Resende (2001)
South African Savanna	4.1	0.18	22.8	32	Scholes and Walker (1993)
Australian Savannas	1.7	0.08	21.3	10	McKeon et al. (1991)
North America Mesquite Savannas	1.2	0.18	6.7		Martin et al. (2003)

high in mesquite savannas of Texas relative to the organic C these soils contain (Tables 4 and 5).

Mineralization/nitrification

In addition to N losses from frequent fires and environmental limitations on biological fixation, high C:N of litter (~60:1) may contribute to low rates of decomposition and mineralization in Cerrado areas, thus maintaining low N availability. The decomposition rate of the litter in a cerrado site was estimated at 2.2 years (Resende 2001). The mean biomass loss was 32% after about 1 year, and immobilization was observed for N, P and S, as their losses of these elements were lower than the biomass loss.

Nutrient use efficiency (NUE) can be estimated as the annual increment of biomass divided by the concentration of nutrients in the litter. A low NUE is usually associated with relatively high soil fertility, whereas a high efficiency may be linked to higher resorption in living biomass (Vitousek 1982). Compared to *Terra-firme* forests, cerrado sites showed higher efficiency for N, suggesting a greater limitation to productivity by nitrogen (Bustamante et al. 2004b).

The rate of net N mineralization in a cerrado site protected from fire was 14.7 N kg ha^{-1} yr^{-1} (Table 5), while in a burned cerrado site it was only 3.8 kg N ha^{-1} yr^{-1}, 1 year after the burning (Nardoto and Bustamante 2003). NH_4-N increased after fire, but no significant changes were observed for NO_3-N. NO_3-N accumulation occurred in short periods during the rainy season in both sites. Data from the same areas after a fire event 2 years later indicated a mineralization of 14.0 kg ha^{-1} yr^{-1} in the unburned cerrado and of 8.9 kg ha^{-1} yr^{-1} in the burned area (Viana 2002). The rates of N mineralization were lower in savannas sites with lower woody density (campo sujo) in the same location. Siqueira (2001) measured rates of 6.6 kg ha^{-1} yr^{-1} in an unburned campo sujo and of 3.8 kg ha^{-1} yr^{-1} in a burned campo sujo.

Table 5. Comparison of nitrogen stocks and fluxes in Cerrado, Llanos and Mesquite savannas of North and South America.

Compartments and fluxes *Major stocks (kg ha^{-1})*	Cerrado[a]	Llanos[b]	Mesquite[c]
Total soil N (0–100 cm)	4576	5850 [i] 4420[b] (0–40 cm)	1900–3200
Aboveground biomass N	54.7[f]	23.7[b]–80.0 [i]	30–112
Belowground biomass N (0–100 cm)	94.5	14.6 [b] (0–30 cm) –40.0[i]	
Major fluxes (kg ha^{-1} yr^{-1})			
N mineralization	14.0		60–140
Atmospheric N deposition	4.2	5–14	8–14
BNF	16–44	12–28	6–35
N gas emissions ($NO + N_2O$)	0.4	0.5–4.0	1.1–3.4
Biomass burning N losses	25.26[g]	8–27	
Other			
% Woody cover	20–50%		42% (s.d. = 12%)
% Herbaceous cover			85% (s.d. = 15%)
Woody plant foliar N (%)	0.7–1.8[e]		3.2–4.1
Herbaceous plant foliar N (%)	0.5–0.6[d]		1.1–1.5
Woody plant root N (%) (0–100 cm)	0.65–0.36 (< 2 mm)[h] 0.75–0.48 (2–5 mm) 0.49–0.20 (> 20 mm)		
Herbaceous plant root N (%)			

[a] Cerrado sensu stricto located in IBGE Reserve, Brasilia, Brazil; [b] *Trachypogon* savannas in Central Venezuela (Medina 1982); [c] Mesquite savannas located throughout Texas, USA (Archer 1989; Asner et al. 2003); [d] Siqueira (2002); [e] Nardoto et al. (2006); [f] Kauffmann et al. (1994) – all living and dead vegetation less than 2 m in height above the soil surface excluding trunks of large trees and shrubs. Grasses comprised 17% of the total N; [g] Kauffmann et al. (1994) – 20.54 kg ha^{-1} lost as particulates, 4.72 kg ha^{-1} lost through volatilization; [h] Nardoto, Bustamante et al., unpublished data; [i] *Axonopus purpusii-Leptocoryphium lanatum* (Barinas Venezuela) (Sarmiento 1984).

Only a small part (~5 kg ha^{-1} yr^{-1}) of the nitrogen content of the grass layer in an African savanna enters through mineralization of the soil organic matter. Most of the N comes from the recycling of the nitrogen stock in dead roots, before humification (~40 kg ha^{-1} yr^{-1}) as the annual bush fire destroys the major part of stems and leaves (Abbadie et al. 1992). This indicates that nitrogen is mostly internally recycled within the vegetation–soil system.

In the cerrado sites the rates of net N mineralization increased during the rainy season while reductions in soil microbial biomass were observed at burned and unburned sites. This suggested a peak of microbial activity with the onset of the rainy season and initial net immobilization followed by net mineralization (Nardoto and Bustamante 2003). This microbial biomass dynamic leads to the accumulation and conservation of nutrients in a biologically active form during the dry period when the activity of the plants is low. At the beginning of the rainy period, nutrients are released and taken up by plants (Singh et al. 1989). In the Cerrado, although net N mineralization and net nitrification rates were highest during the rainy season, inorganic-N concentrations decreased during the rainy season, indicating that plant uptake draws down inorganic-N stocks and consumes the N released from net mineralization (Nardoto and Bustamante 2003).

Despite the transient nature of nitrate in soils, the low content of NO_3-N in soils of the Cerrado sites could be related to low nitrification rates, even though significant production of NH_4-N occurs. Competition between plants and microorganisms for ammonium is probably intense. Hence, the population of nitrifying bacteria may be low in these soils. In soils of the Mediterranean zone and under eucalyptus forests of Australia, similar results were also explained by the low density of nitrifiers found in those soils, and no increase in nitrification after fire was detected (Prieto-Fernandez et al. 1993). Verchot et al. (1999) reported low rates for potential nitrification in a Cerrado area but Poth et al. (1995) detected chemoautotrophic nitrifier populations in Cerrado soils. Nitrifying bacteria could be present but rates of net nitrification and nitrate accumulation are modest. Plants and microorganisms could rapidly take up small increases in NO_3^- production in soil. This is a further indication of N limitation in ecosystems (Davidson et al. 1992).

Similar to the Cerrado, inorganic-N in semi-arid regions of Argentina (Chaco) and the United States (Texas) accumulated in the soil during the dry season, while net N mineralization rates decreased in the same period and increased in the following rainy season (Oliva et al. 1993; Hibbard et al. 2003). Higher microbial immobilization also occurred at the onset of the wet season. In the selective logging sites studied by Oliva et al. (1993), higher N mineralization rates and consequently higher N availability occur as a consequence of the accumulation of dead plant material and increase of light and water availability (Oliva et al. 1993). Increases in N mineralization rates after selective logging are due to increases in soil temperature (high radiation), input of new leaves with lower C:N ratios and reduction in competition for available nutrients between plants and microorganisms.

The effects of different fire frequencies on carbon and nitrogen dynamics of a savanna of the ‘Chaco Semiárido Occidental’ were compared for a single point in time by Gonzalez et al. (2001). Soil was described as a Torriorthentic Haplustoll. Fire frequencies were characterized as: high (one fire every year), medium or normal (one fire every 3–4 years), and low (one fire every 10 years). Organic carbon was lower under the high frequency than under the medium and low frequency areas. Total soil organic carbon, total nitrogen, soil nitrate and soil microbial biomass nitrogen were lower under high frequency fires, although medium and low frequency fires did not differ. Particulate organic carbon and nitrogen were also lower under the high frequency, and were more sensitive than total carbon and nitrogen to the effects of fire history. There were no differences in soil respiration among fire histories. On the other hand, soil respiration and microorganisms were strongly affected in soil samples taken immediately after fire and after periods of 30, 180, 360, and 720 days in a native forest and a grassland in the Chaco region (Chancani Forest Reserve of Cordoba Province) with burned and unburned patches. The conditions observed were stable over the 2 years of study, nevertheless, there was a tendency to recover the original values (Gonzalez et al. 1999). These results showed that repeated burns reduce soil organic matter as well as soil biological activity and may increase soil susceptibility to erosion processes. However, areas under medium or normal fire frequency maintained organic nitrogen and carbon pools and showed higher nitrogen availability.

Beyond the effects of selective logging and fires, the N cycling in the Chaco is markedly influenced by vegetation composition. Soil respiration and soil nitrogen dynamics were measured for 1 year underneath five vegetation types in the Chaco region: a leguminous tree (*Prosopis flexuosa*), a non-leguminous tree (*Aspidosperma quebracho-blanco*), a non-leguminous shrub (*Larrea* spp.), open interspaces, and a pure grassland (Mazzarino et al. 1991a, b). As stated earlier, during the dry season, microbial biomass N and net N mineralization were low, while accretion of easily mineralizable C occurred, but this was reversed with the onset of rain. The highest values of total N, N mineralization, inorganic N, microbial biomass N, density of nitrifiers, N content in litter, total organic C and easily mineralizable C were found under *Prosopis* and the lowest values under shrubs and the interspaces. The main differences between tree species were in N mineralization at the beginning of the wet season, in total and inorganic N pools, and in nitrifier densities; all of which were significantly lower under *Aspidosperma* than under *Prosopis*. N mineralization in the pure grassland was very low despite high values of total N and C sources.

Emissions of NO and N_2O

Nitrification and denitrification are key processes in the production of nitrogen oxides, NO and N_2O (Firestone and Davidson 1989), and low emissions are generally correlated with the dominance of NH_4^+ over NO_3^- (Davidson et al. 2000).

In a recent review, Davidson et al. (2001) concluded that soil emissions of NO from tropical savannas such as the Brazilian cerrado remain a large and important uncertainty. Poth et al. (1995) suggested that Cerrado, burned or unburned, is an important source of NO to the troposphere. However, the high NO production observed by these authors was reported after an artificial water addition in a short-term experiment. Pinto et al. (2002) measured monthly soil fluxes of NO and N_2O in cerrado areas of central Brazil during a year. The study focused on two vegetation types, cerrado *stricto sensu* (20–50% canopy cover) and *campo sujo* (open, grass-dominated), which were either burned every 2 years or protected from fire. N_2O fluxes were very low and below the detection limit in all of the vegetation-fire treatments. Soil moisture and vegetation type were more important in controlling NO fluxes than fire regime (early-dry season, middle-dry season or late-dry season burning). NO emissions increased after burning, but flux returned quickly to pre-fire levels and even lower. In comparison, NO emissions increased 100-fold (to 10.5 ng NO-N cm^{-2} h^{-1}) during a water addition experiment in unburned campo sujo. After the first rains NO fluxes increased to 1.0 ng NO-N cm^{-2} h^{-1} in unburned cerrado and to 1.9 ng NO-N cm^{-2} h^{-1} in burned cerrado. These results demonstrate that wetting of dry soil in the Cerrado causes an increase in NO emissions of a factor of 10 or more, but that the pulse is short lived and does not persist during the rainy season. The annual emissions of N via NO fluxes were similar in the burned campo sujo (0.5 kg N ha^{-1} yr^{-1}) and in the unburned and burned cerrado areas (0.4 kg N ha^{-1} yr^{-1}) while the unburned campo sujo fluxes were the lowest (0.1 kg N ha^{-1} yr^{-1}). A positive relationship between NO emission and soil nitrogen status had been shown for South America savanna soils (Johansson and Sanhueza 1988; Sanhueza et al. 1990; Rondón et al. 1993; Cárdenas et al. 1993) and for savannas of South Africa (Parsons et al. 1996; Levine et al. 1996). However positive correlations between NO emissions and mineralization and nitrification were not found for the Cerrado, although both NO emissions and nitrification rates were low (Pinto et al. 2002).

Similar to Cerrado systems, mesquite savannas of Texas, USA have very low N_2O emissions, but NO fluxes can be relatively high (Table 5), with values ranging from 0.3 kg N ha^{-1} yr^{-1} on dystrophic clayey soils to 2.4 kg N ha^{-1} yr^{-1} on loamy soils (Martin et al. 2003). Many of these savanna-grassland systems in Texas have undergone woody encroachment in the past century or more (Archer 1994), and this has caused substantial increases in NO emissions at both the local and regional scales. Locally, NO fluxes increase by about 200% following increases in woody mesquite cover (Martin et al. 2003). Martin and Asner (2004) used field and remote sensing data to show that the contemporary N cycle of North Texas savannas has a regional NO flux of about 1.6 kg NO-N ha^{-1} yr^{-1}, a value that has probably increased more than threefold in the past 100 years with woody encroachment.

Interactions between N and other elements controlling the N cycle

The N/P ratio in leaves can be used as an indicator of nutrient limitation where N/P < 16 indicates N limitation, values $14 < NP < 16$ co-limitation by N and P and N/P > 16 P limitation (Aerts and Chapin 2000). The mean N/P in leaves of 10 Cerrado woody species (evergreen and deciduous) was 18 indicating a strong P limitation, and although the N resorption rates were similar to the values (30%) presented by Aerts and Chapin (2000), the P resorption rates were much higher ($> 50\%$) Nardoto et al. (2006). The P supply for these woody species seems to be more dependent on biochemical recycling (resorption), whereas N supply is more dependent on N uptake (biogeochemical cycling). Although N and P uptake by plants is low due to the low availability, P limitation is stronger. For example, in a Cerrado area, the flux of N that reaches the soil (bulk precipitation, throughfall and litter leachate) was 9.3 kg ha^{-1} yr^{-1}, whereas for P it was only 0.03 kg ha^{-1} yr^{-1} (Resende 2001).

BNF can, in the long-term, adjust the supply of N close to the availability of other resources, such as P (Schimel et al. 1997). The importance of P availability controlling the N fixation rates is discussed in several studies. In the bacteria, P seems to activate the genes for the nitrogenase synthesis (Stock et al. 1990), and in many cases, the N fixation rates seem to be controlled by soil P availability. As P availability is generally low in the highly weathered soils of the Cerrado (Goedert 1983; Le Mare et al. 1987), this deficiency might be one of the factors limiting the rate of nitrogen fixation in tropical legumes. Data on soybeans indicated that the symbiotic N_2 fixation process has a higher requirement for P than host plant growth (Israel 1987). It is also suggested that symbiotic N_2 fixation has a higher P requirement than the nitrate-assimilation process. These results are consistent with the interpretation that plants solely dependent upon BNF have a higher internal P requirement for optimal growth than plants supplied with nitrate. It can be concluded that P has specific roles in nodule initiation, growth and functioning in addition to its role in host plant growth. Indeed, the whole plant N concentration was significantly greater for plants solely dependent upon BNF than for nitrate-supplied plants when high P concentrations were present in the nutrient solution.

Phosphorus shows low mobility in soil, and the diffusion rate strongly limits its availability to the roots. Mycorrhizal associations can act as important mediators for the transfer of nutrients, and 12 species sampled in a Venezuelan savanna on nutrient-poor soil and dominated by Gramineae and Cyperaceae had arbuscular mycorrhizae (Cuenca and Lovera 1992). Andrade et al. (1996) found in the Venezuelan Gran Sabana colonization by arbuscular mycorrhizae in 18 native species distributed in 7 families. Even in Cyperaceae, generally considered non-mycotrophic, mycorrhizal colonization was observed, demonstrating the importance of these associations in dystrophic soils. Surveys in Cerrado soils indicated that infections of arbuscular mycorrhizae also occur in a large number of native plants (Thomazini 1974; Bononi and Trufem 1983; Siqueira et al. 1989; Miranda and Miranda 1996).

Disturbances/land use changes

Conversion to pastures

The major land-use changes in the Cerrado are conversion to pasture and soybean croplands, but the ecological consequences of these land uses are still poorly understood in Cerrado ecosystems. The introduction of African grasses of the genus *Brachiaria* in the 1970's led to widespread land conversion (Kichel et al. 1996). The region hosts approximately 44% of the national herd, with approximately 50 million hectares of the Brazilian Cerrado planted with African grasses (mainly *Brachiaria* and *Andropogon* spp). Most of the pastures, however, are in an advanced stage of degradation. Generally pure *Brachiaria* or *Andropogon* pastures in the Cerrado suffer a decline in productivity after 4–10 years of grazing (Macedo 1995). The nutrient-poor organic matter produced (6–10 Mg C ha^{-1} yr^{-1} in well-managed pastures; Cadisch et al. 1994a, b) may decrease the sustainability of these pastures, because the scarce nutrients are immobilized and not available for plant growth. The existence of a dense and permanent rooting system within the pasture limits nutrient losses by leaching. The main loss pathways are urine and dung patches in which nutrient concentrations can be very high over a limited area (Boddey et al. 1996).

Studies indicated that BNF could introduce 30–45 kg N ha^{-1} yr^{-1} in *Brachiaria* pastures (Boddey and Victoria 1986; Loureiro and Boddey 1988). This N comes mainly from non-symbiotic associations with endophytic bacteria or bacteria in the rhizophere. Several bacteria such as *Azospirillum*, *Herbaspirillum* and *Gluconacetobacter* can be associated with grasses.

Modifications of soil organic matter and nutrient cycling after land conversion can change the magnitude and direction of NO and N_2O fluxes. The few existing data indicate that the annual emissions of nitrogen oxides are low. Saminêz (1999) measuring soil N_2O fluxes estimated the annual emission in a native cerrado area of 0.52 and of 0.51 kg N ha^{-1} yr^{-1} in a 5-year old pasture (*Andropogon gayannus*). In a 10-year old pasture (*Paspalum* sp.), Nobre (1994) measured fluxes of 0.2 ng N-N_2O cm^{-2} h^{-1}. These authors did not measure NO fluxes, but Varella et al. (2004) compared fluxes of NO and N_2O, soil microbial biomass, and N-mineralization rates in a 20-year old *Brachiaria* pasture of low productivity and in a native cerrado area. Net N-mineralization in the pasture was low, and net N-immobilization was observed in the dry season. Artificial water addition in pastures during the dry season resulted in short-lived pulses of NO (1.3 ng N-NO cm^{-2} h^{-1}). N_2O fluxes were below the detection limit at both sites. Recently, Pinto et al. (2006) compared the fluxes of N oxides in degraded pastures subjected to recovery treatments (fertilization and consortium with the legume *Stylosanthes guianensis*) and a young pasture

(2 years old – formerly a dense cerrado). Considering the measurements between January and April (rainy season), the young pasture emitted 0.03 kg N-NO ha^{-1} versus 0.01 kg N-NO ha^{-1} for the other treatments. In the same period, a cerrado emitted 0.11 kg N-NO ha^{-1}, while a campo sujo showed similar values to the old pastures. Higher fluxes of N_2O (9.5 ng N cm^{-2} h^{-1}) were only measured in the young pasture during the transition from dry to wet seasons.

Conversion to croplands

Soy plantations in Brazil began to expand more vigorously in the second half of the seventies, propelled by expansion in international demand. Expansion affected mainly the states located in the southern region of the country. In 1980, soy had not significantly penetrated the savannas, only about 15% of the soy planted areas in Brazil were outside the southern states boundaries. Ten years later, however, soy plantations formed a continuous zone in central Brazil, largely associated with the expansion of soy in the savannas. The impacts on the regional and global environment of this massive change in land use in only two decades have not been fully assessed.

The expansion of soy was strongly influenced by the existing natural conditions in the savannas, by investments in transport infrastructure and, especially by the development of soybean varieties adapted to the region and highly efficient in N fixation. Today soy is cultivated in the Cerrado (ca. 7 million hectares are used for grain production) without the addition of N fertilizers. It is estimated that 70–85% of the nitrogen in the soy plants comes from BNF (Boddey et al. 1984, 1990). At least 80 kg N (grain + vegetative parts) are necessary for the production of one ton of grain with 6.5% of N. Considering an average production of 2571 kg ha^{-1}, approximately 200 kg N ha^{-1} are needed, and consequently BNF must contribute ~170 kg N ha^{-1}, which is equivalent to 378 kg of urea ha^{-1} (Reis et al. 2003)!

Information on the effects of this input of N in the savanna ecosystems is still very limited. The data now available indicate that the conversion of natural systems to agricultural uses may significantly increase the N_2O emissions. Nobre (1994) has shown that the N_2O emissions have increased during the first 100 days of soy implementation, reaching 0.5 ng N cm^{-2} h^{-1} presumably as a result of the increased N fixation by the cultures. In another study on cultivation of soy in rotation with corn, the emissions during the rainy season varied from 0.8 to 2.5 ng N cm^{-2} hr^{-1} (Saminêz 1999). The relatively dry weather of the Cerrado does not favor high emissions of N_2O, but the increasing use of irrigation can significantly enhance the N_2O emissions.

Another important aspect of soy cultivation in the Cerrado is the link between organic matter management and N cycling. Currently, no-tillage systems are used in about 70% of the soybean cultivated area versus 30% that still use conventional tillage systems. Studies of N cycling impacts associated to soy cultivation should include a survey of the different forms of agricultural management, particularly under no-tillage systems, and their regional distribution and representation.

Over-grazing and fire suppression

In North and South America, Africa, Australia and elsewhere, woody vegetation cover has increased significantly in grazed savannas during the past few decades. Cited causes of woody encroachment include over-grazing of herbaceous cover that reduces competition for woody seedlings, fire suppression that enhances woody plant survival, atmospheric CO_2 enrichment that favors C3 (woody) plant growth, and nitrogen pollution which also favors woody encroachment (Archer et al. 1995). It is noted in most encroachment studies that the woody plants were present somewhere on the landscape prior to the installment of managed grazing. For example, in a South Texas rangeland containing a diverse array of trees, shrubs and sub-shrubs, heavy grazing caused increases in the cover of the nitrogen-fixing tree *Prosopis glandulosa* (mesquite). The same species of mesquite has increased dramatically in cover in a North Texas rangeland during the past century (Asner et al. 2003), but there are very few other woody species established in this region. Most other species are confined to riparian zones, thus few if any woody plants can be found in association with the mesquite cover. Precipitation conditions are similar between the North (650 mm) and South (680 mm) Texas sites, but temperatures are substantially lower in the North, with temperatures below freezing in many months (Asner et al. 2003). Low temperatures in the North likely preclude the presence of many warm-climate woody plants found in the South (*Acacia*, *Diospyros* spp.), and thus the biological and ecological dynamics of woody encroachment are very different between the sites.

Although woody encroachment reduces the quality of land for animal production, in some cases, it enriches total ecosystem C and N stocks (Asner et al. 2004). With the shift to woody vegetation comes a large increase in aboveground NPP and C storage. Increases in aboveground NPP of up to 1400 kg C ha^{-1} have been observed when the dominant woody species is a nitrogen fixer (Geesing et al. 2000). Increases in the aboveground C pool can range from 300 to 44,000 kg C ha^{-1} in less than 100 years of woody encroachment (Asner et al. 2003). When the dominant woody species is a N-fixer, nitrogen accumulation can be 9–40 kg N ha^{-1} yr^{-1} greater in the woody areas than the grasslands (Geesing et al. 2000), with aboveground nitrogen increasing 39–468 kg N ha^{-1} following woody encroachment (Hughes et al. in review).

Conclusions

American tropical and temperate savannas are limited by nitrogen availability. However, land use changes are affecting the savanna N cycles differently in these regions. Grazing and conversion to pasture has been the predominant land use change in most savannas including the Cerrados, although an intensification of mechanized agriculture and irrigation has been observed in the last decade. In the case of the Cerrado and the Llanos, the intensification of fire for pasture management is causing the reduction of woody plant density. Oppositely, in the Chaco and North American savannas, exclusion of fire and grazing are leading to an increase in woody density. In addition, the higher soil P availability in the Gran Chaco and the higher N deposition in North American savannas are resulting in an increase of N cycling and net productivity rates. Besides the impacts of land use changes, some aspects of the N budget for savannas of the American continent are still unclear and require increased analysis of the N fixation rates (both free-living and symbiotic fixers), the spatial and temporal soil heterogeneity controlling N fluxes through soil solution, and the role of riparian zones on N fluxes through streams. Changes in vegetation structure may also have impacts on climate. Hoffmann and Jackson (2000) proposed that the conversion of tropical savannas to grasslands would decrease precipitation but also change the seasonal patterns of rainfall. Biogeochemical cycles in savannas are regulated by seasonal distribution of precipitation and pulses of nutrients resulting from wetting of dry soil which are relevant to maintain the dynamics between microorganism and vegetation. The alteration of seasonal patterns would decouple "supply and demand" processes resulting in higher N losses.

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