AN ABSTRACT OF THE THESIS OF

Elmar Andrade de Castro for the degree of Master of Science in Rangeland Resources presented on June 22, 1995.

Title: Biomass, Nutrient Pools and Response to Fire in the Brazilian Cerrado.

Abstract approved: Redacted for Privacy

Total biomass, total carbon (C), nitrogen (N) and sulfur (S) pools, and fire effects were quantified in four community types of Cerrado *sensu lato*, a Brazilian tropical savanna. These communities varied from grassland (campo limpo), through grassland with sparse shrubs (campo sujo), and woodland savannas (cerrado aberto and cerrado denso). The woodland savannas studied here are variants of cerrado *sensu stricto*, which has a predominant tree layer with shrubs and grasses. Cerrado aberto had a more open tree canopy than cerrado denso.

Total aboveground biomass increased from campo limpo to cerrado denso. Campo limpo had 5,542 kg ha^{-1}; campo sujo, 9,344 kg ha^{-1}; cerrado aberto, 24,847 kg ha^{-1}; cerrado denso, 24,944 kg ha^{-1}. The biomass of each component in the communities (i.e. grasses, herbs, shrubs, trees, litter and woody debris) varied within each community. Campo limpo was mostly comprised of dry grasses (2,021 kg ha^{-1}) and live grasses (1,934 kg ha^{-1}) while cerrado denso had a substantial biomass of trees (12,915 kg ha^{-1}) and shrubs (3,190 kg ha^{-1}). This variability in the biomass of components combined with weather conditions and component moisture content, influenced the fire behavior in each community, which in turn effected biomass consumption. In this study, fire line intensity was lower in grassland (577 kW m^{-1}) than in the woodland (3,693 kW m^{-1}). Biomass consumption for campo limpo was 92 %, and

for campo sujo 84 %. In cerrado aberto and cerrado denso, biomass consumption decreased to 54 % and 33 %, respectively.

Root biomass was quantified up to 2.00 m in depth and classified by diameter classes. Total root biomass in campo limpo was 16,317 kg ha^{-1}, in campo sujo,30,083 kg ha^{-1}; cerrado aberto, 46,584 kg ha^{-1}; and cerrado denso, 52,908 kg ha^{-1}. Root biomass decreased from surface soil to deeper areas in the soil; however, the distribution pattern of root biomass by depth was different for each community. Campo limpo had an abrupt decline after first 10 cm, while cerrado denso had a more gradual decrease to a depth of 2.00 m. Most of the roots (> 71 %) were concentrated in the first 0.30 m of the soil. Root distribution by diameter had great variability among communities. Campo limpo had more fine roots (≤ 0.5 cm), and cerrado denso increased in coarse roots (> 0.5 cm). Total phytomass (aboveground biomass + root biomass) for Cerrado *sensu lato* varied from 19,209 kg ha^{-1} to 73,345 kg ha^{-1}. Roots accounted for more than 73 % of the phytomass. Therefore, the root:shoot ratio in Cerrado *sensu lato* was the highest among tropical forests.

Total nutrient ecosystem pool in Cerrado *sensu lato* ranged from 229,500 to 293,342 kg ha^{-1} for C; 12,500 to 17,862 kg ha^{-1} for N, and 1,566 to 3,721 kg ha^{-1} for S. Nutrients were most concentrated in the soil (>86 %) followed by root pools and aboveground pool. Most of the C, N and S of the phytomass nutrient pools were stored in the roots.

Fire losses of nutrients occurred mostly by volatilization. Campo limpo had the highest losses of nutrients (>90 %) and cerrado aberto had the lowest (<81 %).

Cerrado *sensu lato* had a unique arrangement of nutrient pools. More than 90 % of the nutrients of the total ecosystem were stored in the belowground systems (soil and roots). These results suggest that, in addition to morphological and reproductive plant adaptations to frequent fire in Cerrado *sensu lato*, the conservation of nutrient pools is insured by the fact that such a large portion of it is found in the belowground system.

BIOMASS, NUTRIENT POOLS AND RESPONSE TO FIRE IN THE BRAZILIAN CERRADO

by

Elmar A. de Castro

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed June 22, 1995
Commencement June 1996

Master of Science thesis of Elmar Andrade Castro presented on June 22, 1995

APPROVED:

Redacted for Privacy

Major Professor, representing Rangeland Resources

Redacted for Privacy

Chair of Department of Rangeland Resources

Redacted for Privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for Privacy

Elmar Andrade Castro, Author

DEDICATION

To my father, Manoel Andrade da Silva, and my mother, Margarida Castro Andrade da Silva, who taught me to love and respect nature in a place and time where few others cared.

DEDICATÓRIA

Para o meu pai, Manoel Andrade da Silva e minha mãe, Margarida Castro Andrade da Silva, que me ensinaram amar e respeitar a natureza em um lugar e em um tempo em que poucos se importavam.

ACKNOWLEDGMENTS

I want to thank Dr. J. Boone Kauffman, my major professor for all his interest in tropical ecology, and for the opportunity of doing my field work in the Cerrado of Brazil. I am very glad for the opportunity that he gave me to come to Oregon State University, and besides be a major professor he is also a friend.

I also want to thank Dr. Dave Pyke and Dr. Ron Nielson for their help, inputs, and interest in my work. Thanks to Dr. Patsy. Miller for reviewing my last chapter.

Thanks to Fulbright Commission/Laspau for the financial support, and to the USDA Intermountain Research Station for providing much of the funding for this research.

My field work could not have been completed if I did not have the help of Boone, João Dias, José Carlos, Inês, Medina, and Anselmo. I am also indebted with to the "Corpo de Bombeiros", who were in charge of the prescribed fire, and the "guardinhas" of IBGE Ecological Reserve, who gave me early and late rides to Brasilia. Thanks to the administrators of the Reserve, particularly Iracema Gonzales for logistic support. Ron Babbitt and Bento Barros also insured a very nice field work environment. Thank you all very much.

Thanks to Dian Cummings, Boone Kauffman, Ron and Barbara Shea who made my life much easier when I first got here. Special thanks to Cathy Pendergrass for all the fun weekends. Corvallis would not be the same without her.

Thanks to Flint and Annalee Hughes for the long nights of talking, introduction of Spike Lee, good music, and good food. I will miss our good times, the house and Marin.

I want to thank the fellow graduate students and friends including, Cheshire Mayrsohn, Daniela Roth, Richard Case, Pedro Gonzalez, Nick Otting, Danna Lytjen, Mack Barrington, and Heather Miller, all of them contributed with a word of encouragemnt and a friendly smile.

I could not forget Ieda Mendes and Walfrido Tomas for their friendship.

Finally, I do not have any words to express myself how much I am grateful to Fernando Barros. His love, care, and patience allowed me go through the experience of being back at school and finishing up all this work.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX FIGURES

BIOMASS, NUTRIENT POOLS AND RESPONSE TO FIRE IN THE BRAZILIAN CERRADO

CHAPTER 1
INTRODUCTION

Tropical savannas are distributed between the Tropic of Cancer and the Tropic of Capricorn in Central America, South America, Africa, South Asia, and Australia. Savannas cover approximately 13 % of the terrestrial land surface (Bolin et al. 1993). They are characterized by pronounced dry and wet seasons, a distinct structure comprised of grass and tree layers, and the presence of frequent fires (Bourlière 1983). In South America, tropical savannas occupy 250 million ha. Brazil contains 80 % of South American savannas, followed by Colombia with 8% and Venezuela with 5% (Fisher et al. 1994). The other 7 % is found in Bolivia, Surinam and Guyanas. In Venezuela and Colombia, tropical savannas are referred to as Llanos (Blydenstein 1962 1967, Silva et al. 1971, Sarmiento 1983), while Cerrado is the commonly used term in Brazil (Goodland 1971, Coutinho 1976, Eiten 1978, Sarmiento1983, Kauffman et al. 1994).

Cerrado *sensu lato* (s.l.), or simply Cerrado includes plant communities of different compositions and structures, varying from grassland to forest (Eiten 1972) (Figure 1.1.). It has been classified by physiognomy (Eiten 1972, Coutinho 1976), and quantified in terms of tree density, height and basal area (Goodland 1971). The most common vegetation communities defined and classified by these authors are:

campo limpo: a pure grassland nd totally absent of trees. The flora here is often similar to the surface layer of woodland community types. In the bottom part of valleys, campo limpo usually has a shortage of water in the dry season and an excess of water during the rainy season

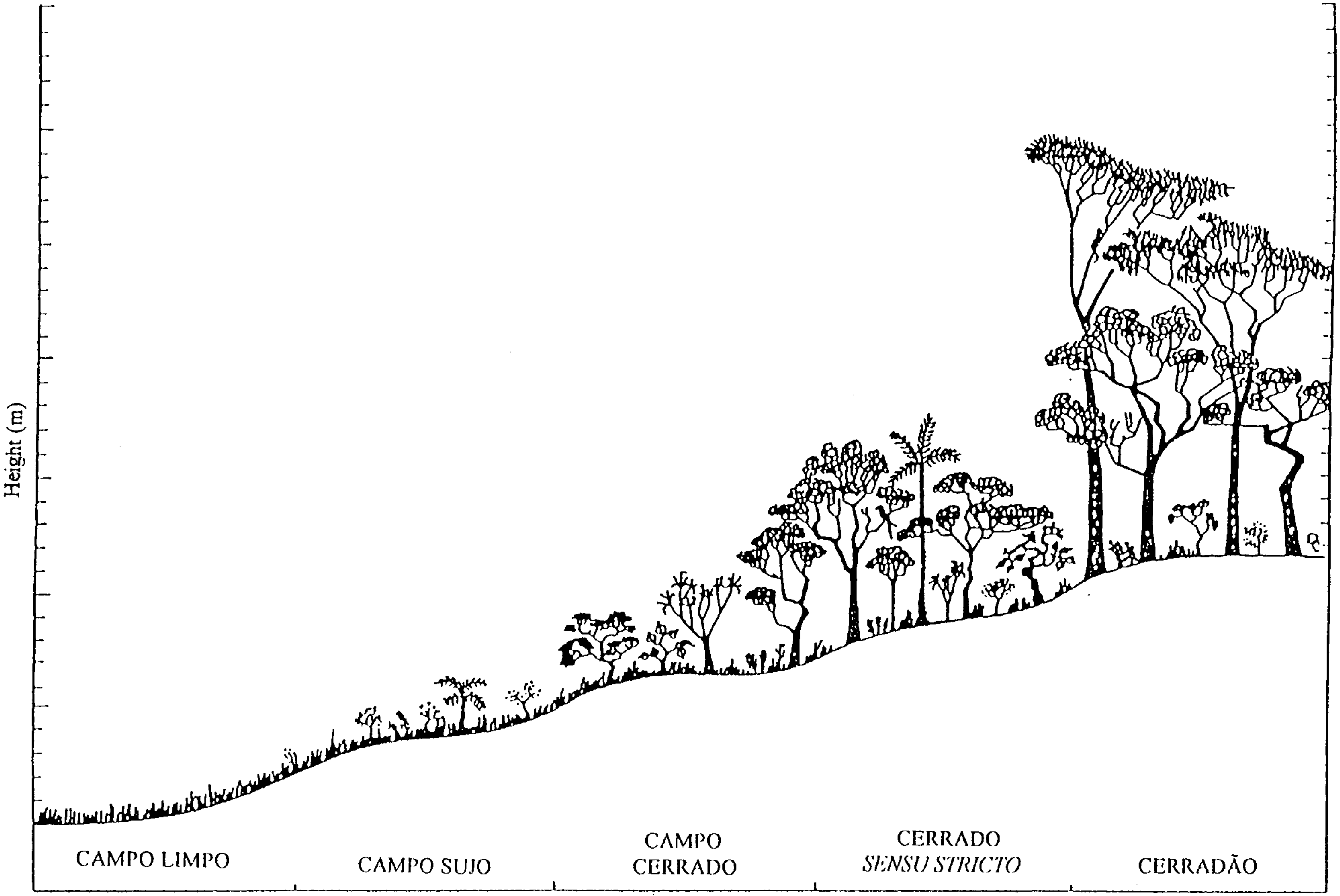


Figure 1.1 Cerrado *sensu lato* vegetation gradient (Courtesy: Dian Cummings).

campo sujo: a grassland with few scattered shrubs, and acaulescent palms. Woody plants in this community may reach 3.0 m. Tree density is less than 1000 ha^{-1}, and total basal area is 3 m^2 ha^{-1};

campo cerrado: an open savanna/woodland. Overstory cover is < 30-40 %. Trees and shrubs occur over a continuous layer of grasses and herbs. Average tree height is 4 m, tree density is 1400 ha^{-1}, and total basal area is 7.6 m^2 ha^{-1};

cerrado *sensu stricto* (s.s.): a tree-dominated plant community with an overstory covering 30-40 %. Grass and herbs are also found in this community. Mean tree height is 6 m. Tree density is approximately 2000 ha^{-1}, and total basal area is 16.8 m^2 ha^{-1};

cerradão: a medium-tall arboreal form with a closed or semi-closed canopy. In general, grasses, herbs and shrubs are sparse or absent. Canopy cover can be more than 50 %. Height of trees is 9 m and tree density is 3000 trees ha^{-1}. Total basal area is 30.0 m^2 ha^{-1}.

The Cerrado vegetation mosaic occupies 1.5 million km^2 in continuous area of the central part of Brazil. Patches of Cerrado s.l. are distributed in the Amazon tropical rain forest (the northern and western limits); in the Caatinga, a tropical dry forest (the eastern limit); and in the Pantanal, a wetland (the southwestern limit) (Coutinho 1990). The total Cerrado area covers approximately 1.8 million km^2 or 23 % of the Brazilian territory (Figure 1.2.). Cerrado s.s. is the most common community type, comprising 65 % of the total Cerrado s.l. area (Haridasan 1990). Campo cerrado, campo sujo, and campo limpo comprise together 12 %, and cerradão covers another 12 % (Adamoli and Azevedo 1983 cited in Adamoli et al. 1987). The remaining 11 % is distributed in riparian areas, mesophytic forests, and other small plant communities.

Climate has been suggested as the most influential factor contributing to the composition and formation of Cerrado s.l. (Eiten 1972, 1992). Precipitation ranges from 1300 to 1800 mm. The dry season extends from April to August and the wet season from September to March. Mean relative humidity varies from 38 to 96 %. Temperature, in

Figure 1.2. The distribution of Cerrado *sensu lato* vegetation in Brazil.

contrast is more constant throughout the year. The maximum average temperature is 25 °C and the minimum average temperature is 21 °C (Ab'Saber 1983). According to the Köppen classification (DNER 1976), Cerrado s.l. is AW climate type. Elevation is between 300 and 1700 m.

The majority of soils are Latosols, classified in the American soil taxonomy as Oxisols, and Ultisols. Soils are nutrient poor, dystrophic with low capacity of cation exchange, high concentration of aluminum, and pH varying from 4.0 to 5.0 (Eiten 1972, Lopes and Cox 1977, Adamoli et al. 1987, Haridasan, 1990). Soils are deep, with few differences in horizons, and colors varying from red to yellow. Soils are well drained, highly weathered and leached. Primary minerals are absent, and there is a predominance of oxides and hydroxides of iron and/or aluminum (Adamoli et al. 1987).

In addition to climate and soil conditions, fire has contributed to the vegetation composition and structure. Charcoal from the Cerrado is dated to 8600 years B.P. (Coutinho 1981). Records of indigenous populations using fire for hunting, war, and rituals are common (Magalhães 1913, Eiten 1975). The indigenous Kaiapos population still uses fire as a management tool to control snake and scorpion populations near settlements. Fire is applied just after the beginning of fruit formation of pequi (*Caryocar brasiliense* Cambess., Caryocaraceae) to insure that any pequi flower, a potential fruit, is not lost in fire consumption (Anderson and Posey 1987).

Plant adaptation to frequent fires is remarkable in this ecosystem. Basal and epicormic sprouts are common in trees and shrubs. Underground organs are common in the herbs, shrubs, and trees of Cerrado s.l. (Furley and Ratter 1988). Anomalous arrangement of meristematic tissues occur in palms, graminoids and velloziaceas (Rachid-Edwards 1956). Trees have a wide and high canopy and usually are not directly affected by fire. They also have a very thick trunk bark protecting the cambial meristematic tissues. Mortality of vegetation caused by fire is generally low and insignificant (Ramos 1990). Fire return interval increases from grassland to woodland. However, fire rarely penetrates the cerradão forests (Eiten 1972, Goodland and Ferri 1979).

Grasses are predominantly from the C4 pathway, but C3 grasses tend to increase in the woody savannas (Filgueiras per. comm.). Ninety four percent of herbs are perennial (Warming and Ferri 1973, Coutinho 1978b). More than 700 woody species have being identified for all Cerrado s.l. Herbaceous and small shrubs species richness are approximately 127, and a total of 108 grasses and 54 orchids have been identified in the Cerrado (Heringer et al. 1977). Studies of plant community in Cerrado vegetation indicate a high beta diversity in cerrado s.s. flora (Ratter and Dargie 1992, Felfili and Silva Jr. 1993). Environmental factors, such as local fires, poor soil drainage, man-made disturbance (Gibbs et al.1983), soil fertility (Goodland and Pollard 1973), and topography (Oliveira-Filho et al. 1989) influence the distribution of communities within Cerrado s.l..

Similar to other tropical biomes, Cerrado s.l. is threatened by anthropogenic activities which may permanently alter plant composition, structure, productivity and overall biological diversity. The increasing of agriculture crops (e.g. soybeans, corn, and rice) results in deforestation of large areas of the Cerrado (Coutinho 1982). Moreover, the Cerrado is exploited to produce charcoal for steel companies (Felfili and Silva Jr. 1993). Urban settlements, dams, cultivated pastures, crop fields and degraded areas are estimated in 37 % of Cerrado area (Dias 1990). Projections for the year 2000 indicate that a total of 49 % of Cerrado land surface will be cleared for main crops, cultivated pastures and open areas (Nepstad et al. 1995). Only 1.5 % of the Cerrado is protected in the Brazilian park and reserves systems (Dias 1990).

Numerous studies of Cerrado vegetation ecology, and taxonomy have been carried out (Goodland and Ferri,1979, Filgueiras et al. 1993, Felfilli and Silva Jr.1993), there have been few studies of carbon and nutrient pools, or fire ecology (Coutinho, De Vuono, and Lousa 1978, Batmanian and Haridasan 1985, Kauffman et al. 1994).

Fire affects the vegetation, soil, fauna, nutrient cycling, alters energy flows and influences the atmosphere (Gillon 1983, Frost and Robertson 1985). Because of the great frequency and large areal extent of tropical savannas, fires in this ecosystem may contribute as much as one-third of all CO_2 arising from biomass burning sources (Crutzen and Andreae 1990).

The frequency, severity and size of fire are factors which define the fire regime in an ecosystem (Agee 1990). In Southern Africa, fire return interval of one to five years has been described (Huntley 1982; Trollope 1978, 1982). For campo limpo, estimations are one to two years and for campo cerrado three to five years (Eiten 1972, Coutinho 1979, Pivello and Coutinho 1992).

Fires in savannas are characterized as surface fires with a low flame height (Frost and Robertson 1985). Description of fire behavior is scarce for fires in Cerrado vegetation. Kauffman et al. (1994) determined the flame depth (1.7 to 9.7 m), flame angle (48^{o} to 61^{o}), flame length (2.7 to 5.4 m), flame height (1.8 to 3.7 m), rate of spread (1.4 to 30.0 m min. $^{-1}$), residence time (15 to 26 s), and fire line intensity (2842 to 16,394 kW m^{-1}) for fires in Cerrado communities near Brasilia, DF.

The quantities of nutrients released by fire depend upon factors, such as the quantity of biomass consumed, fireline intensity, the type of vegetation, and its concentration of nutrients in leaves, stems and other locations most susceptible to combustion (Frost and Robertson 1985, Coutinho 1990). Some nutrients are easily volatilized (e.g. N and S) while others are mostly deposited on the soil surface as ash or remain as residual material not consumed by fire (Frost and Robertson 1985, Kauffman et al. 1994). In Cerrado vegetation, nutrients such as Ca, K, P and Mg increase in availability in the upper 5 cm of soil following fire (Coutinho 1982, 1990). Inputs of nutrients from precipitation in campo cerrado in São Paulo state were recorded monthly by Coutinho (1979), who found that deposition is greater in the wet season when precipitation increases. However, there is also a contribution of nutrients via dry fall during the dry season. In the same study area, Pivello and Coutinho (1992) reported great losses of N and S during fires. Near Brasilia, DF, the amount of N, C, and S lost by fire decreases along vegetation gradient from campo limpo to cerrado s.s.. In campo limpo most nutrients are lost by volatilization, but in cerrado s.s. the greater amount of nutrients are lost via particulate transport. For all communities, C, N, and S are the nutrients lost in the highest quantities (Kauffman et al. 1994).

The structure and arrangement of materials as well as moisture content are factors influencing levels of biomass consumption. Kauffman et al. (1994) quantified fuel loads in Cerrado vegetation at the IBGE Ecological Reserve. Fuels ranged from 7 Mg ha^{-1} in campo limpo to 10 Mg ha^{-1} in cerrado s.s. (tree biomass > 2.0 m in height was not included). These values are low when compared with slashed fuels in tropical dry forest (Caatinga, 74 Mg ha^{-1}) and tropical rain forest (290 to 435 Mg ha^{-1}) (Kauffman et al. 1993, 1994). Fuel biomass consumed by fire (the combustion factor) in Cerrado is 100 % in campo limpo, 97 % in campo sujo, 71 % in campo cerrado, and 84 % in cerrado s.s.(Kauffman et al. 1994). The combustion factor in tropical dry forest ranges from 74 to 88% and tropical primary slashed rain forest range from 42 to 57 % (Kauffman et al. 1993, 1995).

While a few studies of aboveground biomass exist, studies of root biomass in Cerrado vegetation are nonexistent. However, individual root systems of species have been classified into deep, medium or surface depth classes (Rawithscher 1948). Subterranean organs were described by Rizzini and Heringer (1961, 1962).

Root systems in African savannas are well developed, and penetrate deeply into the soil. However, the majority of belowground biomass is located in the upper 30 cm of the soil surface. In addition, the root systems of herbaceous and woody plants are greater in biomass than aerial parts (Menaut and Cesar 1979). Shrubs and trees are characterized as having a tap-root with well developed lateral roots (Hopkins 1962). Mean root biomass in the forest-savanna mosaic in Lamto, Ivory Coast, varies from 10.1 to 10.0

Mg ha^{-1} in contrast to aboveground biomass which range from 3.3 to 4.4 Mg ha^{-1} (Lamotte 1978). In South America, Sarmiento and Vera (1979) determined that maximum root biomass range from 1.2 to 1.9 Mg ha^{-1} in an area of western Venezuela llanos.

Carbon nutrient concentration in Cerrado s.l. has been estimated in the range from 0.4 % to 4.6 %, while nitrogen concentration ranges from 0.04 to 0.23 % (Goodland and Ferri 1979), and sulfur supply is low (McClung and Freitas 1959). A carbon/nitrogen ratio of 11.2 has been reported for Cerrado s.l. of Mato Grosso state (Askew et al. 1970). Soil nutrient pool studies are scarce for Cerrado s.l. Kauffman et al. (1994) determined a range of 656 to 1,670 kg ha^{-1} for the soil nitrogen pool to a depth of 0.10 m in the gradient campo limpo to cerrado s.s.. Total ecosystem pool for any other tropical savanna has not been determined to date.

In order to understand the nutrient pools, structure, fire ecology and effects on Cerrado vegetation, three studies were undertaken. Objectives of these studies were to (a) quantify total aboveground biomass, fire behavior, and biomass consumption, (b) quantify the structure and total root biomass of plant communities, and (c) quantify ecosystem C, N, and S pools and dynamics along a vegetation gradient in the Brazilian Cerrado.

CHAPTER 2
TOTAL ABOVEGROUND BIOMASS, FIRE BEHAVIOR, AND BIOMASS CONSUMPTION ALONG A VEGETATION GRADIENT IN THE BRAZILIAN CERRADO

Abstract

Aboveground biomass, fire behavior and consumption were quantified in a Cerrado *sensu lato* (s.l.), vegetation gradient from grassland (campo limpo) to a woodland with closed shrub and more scattered trees (cerrado *sensu stricto*) in Brasilia, DF, Brazil. Total aboveground biomass increased from campo limpo (5,542 kg ha^{-1}) through campo sujo (9,344 kg ha^{-1}), cerrado aberto (24,847 kg ha^{-1}) and cerrado denso (24,944 kg ha^{-1}) (The latter two communities are variants of Cerrado *sensu stricto*). Components varied among communities, trees were non existent in campo limpo but had a biomass of 12,915 kg ha^{-1} in cerrado denso. Conversely, grasses declined along the gradient from 3,955 to 1,600 kg ha^{-1}. This variability influenced the fire behavior, consumption and subsequent plant recovery. Fireline intensity increased from campo limpo (557 kW m^{-1}) to cerrado denso (3,693 kW m^{-1}). Consumption in campo limpo and campo sujo was 95.6 % and 98.7 %, respectively. In cerrado aberto and cerrado denso, some shrub stems and trees remained after fire; consumption in these communities was 72.6 and 66.1 %, respectively.

Total biomass in Cerrado *sensu lato* (s.l.) had not been previously measured. The results of this study indicate that compared to other Brazilian tropical ecosystems such as, tropical dry forest and tropical rain forest, Cerrado has the lowest aboveground biomass. However, biomass is high compared to other tropical savannas of the world.

Introduction

Cerrado *sensu lato* (s.l) ecosystem is a diverse tropical savanna with a vegetation gradient ranging from pure grassland (campo limpo) through grassland with small and sparse shrubs (campo sujo), an open savanna/woodland (campo cerrado), savanna woodland dominated by shrubs and trees (cerrado *sensu stricto*), and a closed canopy forest (cerradao) (Coutinho 1976). This ecosystem comprises 1.8 million km^2 in the central part of Brazil (Ab'Saber 1983). Execed in size only by the Brazilian Amazon tropical forest (Furley and Ratter 1988). It is characterized by distinct tropical wet and dry seasons, classified as AW by Köppen (Sarmiento 1983, DNER 1976), and by a constant temperature through the year. Soils are deep, well drained, and low in mineral nutrient concentration and pH. They have a low base saturation and a high concentration of aluminum (Eiten 1972). Climate and soil conditions combined with frequent fires have been suggested as determinants of Cerrado s.l. vegetation in Brazil (Eiten 1972, Coutinho 1990).

Fire has been an ecosystem disturbance in the Cerrado for millennia (Eiten 1972, 1975). The oldest recorded charcoal is dated at 8600 years B.P. (Coutinho 1981). Berger and Libby (1966) found charcoal pieces near Brasilia, DF dated about 1600 years B.P. Indigenous people of the Cerrado had many traditional uses for fire such as for hunting, agricultural purposes, myths, festivals and war (Magalhães 1913, Eiten 1975, Coutinho 1982). Currently, fire is used as a management tool for increasing vigor of pasture grasses for livestock, deforestation and clearing of large areas for agricultural purpose, pest control, and may also occur accidentally (Goedert 1983, Coutinho 1992). The majority of fires occur at the end of the dry season. Principal ignition sources are humans and more rarely lighting (Coutinho 1990).

The structure, physiognomy, and floristic composition of this ecosystem appears to be well-adapted to or even dependent upon fire (Coutinho 1982). Graminoids provide a combustible fuel source and are well represented in Cerrado vegetation types. Following fires, graminoids recover rapidly because their basal meristems are protected by green leaf sheaths, or soils (Rachid-Edwards 1956). In addition to plants of Poaceae and Cyperaceae, Bouillenne (cited by Rachid-Edwards, 1956) reported similar adaptive traits for plants of the Velloziaceae, and Bromeliaceae, which are common families in Cerrado s.l.. Shrubs and perennial herbs have the capacity to sprout from subterranean tissues, even if all aboveground biomass is consumed by fire (Eiten 1972). Trees have thick bark to protect their cambial tissues (Eiten 1975) from thermal damage (Coutinho 1990). Some trees such as *Aspidosperma tomentosum* Mart. (Apocinaceae) have dormant apical buds that are protected by dense and hairy leaves (Coutinho, 1990). If those apical buds are killed by fire, adventitious buds may produce epicormic sprout. The occurrence of a long dry season and low relative humidity in combination with these biological and ecological traits result in an ecosystem very susceptible yet adapted to fire.

The fire return interval has been determined to be as frequent as once a year in grasslands (Eiten 1972), and three years for campo cerrado (Pivello and Coutinho 1992). Eiten (1975) estimated the average frequency of fire set by indigenous people of the Cerrado area, Mato Grosso, Brazil, to be three to five years.

Few studies in Cerrado vegetation quantified biomass, or described fire behavior. Biomass of herbaceous layer was quantified by Cesar (1980) and Cavalcanti (1978) but components were not partitioned. gramineous and non-gramineous biomass of herbaceous layer of campo cerrado was determined (Batmanian 1983). Post fire biomass increases were investigated the following year in campo sujo (Rosa 1990). Comparison of biomass, fire behavior and effects of fire on consumption in Cerrado s.l. were reported by Kauffman et al. (1994), although trees were not included in their survey. Thus, total aboveground biomass (TAGB) in communities of Cerrado s.l. has not been described. Vegetation biomass may contain a great amount of stored C; deforestation and burning promote loss of this C to the atmosphere. Therefore, quantification of TAGB and biomass consumption by fire is of great importance to understand C dynamics, and its contribution to the increase in CO_2 in the atmosphere.

Objectives of this chapter were to (1) quantify total aboveground biomass before fire, in a gradient from open grassland to a dense woodland; (2) partition the biomass into meaningful components in each community type based on plant morphology, ecosystem structure and influences on fire behavior; (3) describe fire behavior in each community; and (4) determine post fire biomass and biomass consumption by fire.

Study Site

The research was conducted at the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatistica (IBGE Ecological Reserve) and at the Estação Ecológica do Jardim Botânico de Brasilia (JBB Ecological Reserve). They are located approximately 35 km south of Brasilia, DF, in Brazil (15^{o} 51' S and 47^{o} 63' W). The elevation is 1,100 m and slopes are < 10%. During the period from 1980 to 1992, mean annual temperature varied from 19.2 °C to 22.4 °C. Mean precipitation was 1482 mm distributed in two distinctive seasons; the wet season from October to March had 1257 mm and the dry season extended from April to September with 225 mm. Mean maximum relative humidity was 81% in December and the mean minimum was 55% in August (File data from Estação Agroclimatologica do IBGE 1980-1992).The IBGE and JBB Ecological Reserve vegetation is characterized by a mosaic of communities ranging from grassland to closed-canopy forest. At the IBGE Ecological Reserve 1,100 plant species distributed among 135 botanical families have been identified (IBGE internal publication). The most common families are Leguminosae, Asteraceae, Poaceae, and Orquidaceae; a number of rare species are present in the composition; endemism is common.

Among the fauna some animals such as, the giant ant eater (*Myrmecophaga tridactyla* Linnaeus), veado campeiro *(Ozotoceros bezoarticus* Hamilton-Smith*)*, and lobo guara (*Chrysocyon brachyurus* Ameghino*)* are in danger of extinction (IBGE internal publication, Alho 1990).

In this study, the biomass and structure of four community types was investigated, (campo limpo at IBGE Ecological Reserve and campo sujo, cerrado aberto and cerrado denso at the JBB Ecological Reserve). Cerrado aberto and cerrado denso are variant of cerrado *sensu stricto.* Cerrado aberto was characterized by a more open canopy cover compared to cerrado denso. Currently, the study areas are part of a biennial fire treatment in a study about fire effects on Cerrado vegetation.

Methods

Aboveground biomass was partitioned into components based upon plant morphology, influences on fire behavior, approaches necessary for the quantification of biomass. In each plant community, four clusters of six transects were established (Appendix 2.1.). Each transect was 15 m in length. Downed wood debris was quantified along all transects (n=24). Other components were measured in four transects in the same cluster. The first cluster was randomly established and the others were systematically set 50 m apart. Aluminum stakes marked each end of the transect to ensure their exact relocation after fire.

Downed wood debris

Downed wood debris was quantified in cerrado aberto and cerrado denso using the planar intersect method (Van Wagner 1968, Brown 1971, Brown and Roussopoulos 1974). This component was not present in the campo limpo and campo sujo grasslands. The planar intersect method consists of measuring all dead wood material that intercepts a transect. Diameter size classes were based upon the standard timelag classes described by Deeming et al. (1977). These classes are 0 to 0.64 cm in diameter (1-hr timelag fuels), 0.65 to 2.54 cm in diameter (10-hr timelag fuels), 2.55 to 7.6 cm in diameter(100-hr timelag fuels) and > 7.6 cm in diameter (1000-hr timelag fuels). The timelag constant is the time period required for a wood fuel particle within those diameter classes to lose 63% of its initial moisture content when placed in an equilibrium of standard laboratory conditions of 27 °C and 20% relative humidity (Pyne 1984). In this study, wood debris > 7.6 cm in diameter was not encountered in the communities surveyed. The 1-hr timelag fuels were inventoried along the first 5 m of the transect; 10-hr fuels were measured from 0 to 10 m, and the 100-hr fuels were measured along the entire 15 m transect. Biomass was calculated utilizing the following formula :

$$WD_{biomass} = \left(\frac{N * \pi^2 * sec * d^2}{8 * L}\right) * S$$

where:

$WD_{biomass}$= Weight per unit area (g cm^{-2}),

N = Total number of wood debris intersections,

sec = Wood debris angle correction factor (degree) ,

S = Specific gravity (g cm^{-2}),

L = Length of sample plane (cm), and

d = Quadratic mean diameter (cm).

For each size class, a quadratic mean diameter, angle correction factors and specific gravity were based on data collected specifically for these communities (OSU file data). Slope correction factor in the original formula (not shown here) was not needed due to the level topography in all communities. After fire the transects were remeasured to quantify residual plant materials that were not consumed or deposited because of fire.

Herbaceous stratum, litter, and ash.

The herbaceous stratum contained hard wood litter, green and dry graminoids, dicots less than 1.0 cm in diameter and/or those with main stems >1 cm in diameter, but less than 0.50 m in height, and terrestrial members of the Bromeliaceae and Palmae.

All materials within a 0.25 X 0.25 m microplot placed at 5 and 10 m along the 4 central transects were collected, and then overdried at 60 °C for 48 hr (n=32 plots per community). Ten samples from each community were randomly selected for separation into the components listed above. The ratio of each component to the total mass was calculated through separation of 10 randomly selected microplots in each community. The average ratio of each component was used to calculate composition and mass for all samples. Post-fire mass of this layer was collected along each transect at 6 and 11 m, employing the same methods as pre-fire sampling.

Ash mass was calculated through collection of all ash in a 0.50 X 0.50-m plot at 6 m on each central transect (n=16). Ash was collected using a vacuum cleaner and electric generator.

Shrubs

All shrubs with a main stem >1.0 cm in diameter, and > 0.50 m in height but < 2.00 m in height were measured in a 1 X 5-m belt transect established adjacent to the transects. The height and elliptical crown diameters of all shrubs in each plot were measured. The elliptic crown area for each shrub was calculated applying the equation:

$$A=\left(\frac{W_1 * W_2 * \pi}{4}\right)$$

where:

A= Elliptic crown area (m^2),

W_1= Longest diameter crown (m),and

W_2= The longest crown diameter perpendicular to W_1 (m).

Crown volume was calculated by multiplying elliptic crown area by height. From these data, biomass of shrubs was calculated through multiple regression analysis developed by Kauffman (Appendix 2.2). After fire, the same plots were remeasured utilizing the same methods.

Trees

All individual trees (> 2.0 m in height) in a 3 x 15-m plot established adjacent to the transect were measured for diameter and height. Diameter measurements were taken at height of 0.30 m and 1.30 m. These measurements were made because most studies in Cerrado refer to a basal area at 0.30 m (Silberbaur and Eiten 1987, Ramos 1990, Sambuichi 1991, Felfili and Silva Jr. 1993). Thus, the basal area calculated in this study can be compared with the results of other studies. However, equations used for the calculation of tree biomass were based on the diameter at 1.30 m. Tree density per hectare, and mean and range of heights were also calculated. Tree biomass was calculated using the equation presented by Brown et al. (1989) for tropical forests. The regression chosen was for trees of the moist life zone; diameter and height were independent variables. Although this equation was not developed specifically for Cerrado trees, it was judged to be the most applicable. Dr. S. Brown (per. comm.) stated that these equations are very robust; therefore this study provides a preliminary estimate of tree biomass whose accuracy has not yet been determined.

Fire behavior

Weather conditions including ambient temperature (°C), relative humidity (%), wind speed (m s^{-1}), direction, and cloud conditions were measured immediately before burning. Fires were ignited as perimeter or circle fires. However, the campo limpo was lighted with a backfire pattern (against the wind), because of high wind speeds at the time of ignition.

Flame characteristics were measured for each fire. At least three random observations of fire behavior were recorded including flame length (distance between the tip of the flame and the ground midway in the zone of active combustion), flame height (vertical distance from the ground to the top of the flame), flame depth (distance at the base of the flame from the leading edge to the rear edge), and flame angle (angle formed between the flame front and the unburnt fuel bed measured off the horizontal) (Appendix 3.2.). In addition, the rate of spread (m $min.^{-1}$), which is the forward rate of movement of the flame front; and residence time (s), which is the length of time for the fire front to pass a point were recorded (Rothermal and Deeming 1980).

With these data, fireline intensity (kW m^{-1}), which is the energy or heat output from flame length of fire front (Bryan 1959), was determined using the formula:

$$I = 258\, F_L^{2.17}$$

where:

I = Fireline intensity (kW m^{-1}), and

F_L = Flame length (m).

Reaction intensity (kW m^{-2}), which is the rate of heat released per unit area in the active combustion zone, was calculated from:

$$I_R = \frac{I}{D}$$

where:

I_R = Reaction intensity (kW m^{-2}),

I = Fireline intensity (kW m^{-1}), and

D = Flame depth (m).

Moreover, heat per unit area, defined as the direct heat on the surface was calculated (Rothermel and Deeming 1980 and Alexander 1982) from:

$$H_A = \frac{60\, I}{R}$$

where:

H_A = Heat per unit area (kJ m^{-2}),

I = Fireline intensity (kW m^{-1}), and

R = Rate of spread (m min^{-1}).

Moisture content

Samples to determine moisture content of vegetation and the soil surface were collected before burning. Samples were placed in an air-tight soil container and weighed in the field to determine fresh weight. In the lab, samples were dried at 100 °C for 24 hours and reweighed to determine dry weight. Moisture content was determinate on a dry weight basis, applying the equation:

$$MC = \left(\frac{fw - dw}{dw} \right) * 100$$

where:

MC = Moisture content (%),

fw = Field weight (g), and

dw = Dry weight (g).

Analysis of Variance (ANOVA) was applied to test for differences in total biomass and in the individual components of biomass among plant communities. I found that means were correlated positively with the variance (i.e. greater means were followed by greater variance). Therefore, data were log-transformed prior to analysis (Sokal and Rohlf 1981). However, results of the ANOVA with log-transformed data were not different from original data at 90 % of confidence level, so results are presented here without the transformation. If significant differences in communities were found, the least significant difference, a multiple range test, was applied, and differences among communities determined (p-value = 0.10).

Results

Pre-fire biomass

Pre-fire total aboveground biomass (TAGB) in this study increased significantly from the grassland (campo limpo and campo sujo) to the woodland communities (cerrado aberto and cerrado denso) (Table 2.1.). The composition of aboveground biomass varied among communities. Total graminoids (live and dormant grass combined) were significantly greater in the campo limpo and campo sujo grasslands than in the cerrado aberto and cerrado denso. Biomass of graminoids in campo limpo accounted for 72 % of its TAGB, while in campo sujo, it accounted for 45 %. In contrast, cerrado aberto and cerrado denso had 8 % and 7 % graminoids, respectively (Table 2.1., Figure 2.1.). Cerrado aberto and cerrado denso had significantly greater litter biomass than campo limpo and campo sujo. Litter in campo sujo comprised the greatest proportion of its total biomass (Figure 2.1.). Biomass of small dicots, palms and bromeliads was significantly higher for cerrado aberto than for other communities (Table 2.1.). Dead downed wood debris was not present in the grasslands. Total wood debris comprised 7 % of TAGB of cerrado aberto and cerrado denso (Table 2.1.).

Cerrado aberto had the highest shrub density, mean height, height range, basal area per tree, and basal area per hectare followed by cerrado denso and campo sujo (Table 2.2.A). Consequently, cerrado aberto also had the highest shrub biomass (Table 2.1.). Tree density was also highest in cerrado aberto; however, height (mean and range), individual basal area, and basal area per hectare were lower than in cerrado denso (Table 2.2.B). Tree biomass was statistically greater for cerrado denso (12,915 kg ha^{-1}) than for cerrado aberto and campo sujo. (Table 2.1.)

Table 2.1. Total aboveground biomass (kg ha^{-1}) before, after fire, and combustion factor (%) along a vegetation gradient in Cerrado near Brasilia, DF, Brazil (August-October, 1993). Numbers are mean ± standard error.

component	campo limpo			campo sujo			cerrado aberto			cerrado denso		
	pre fire	post fire	C. factor	pre fire	post fire	C. factor	pre fire	post fire	C. factor	pre fire	post fire	C. factor
HERB LAYER												
dicot litter	629 ±57 a	0	100.0 ±0.0	1,907 ±311 b	0	100.0 ±0.0	3,809 ±306 c	7 ±7	99.9 ±0.1	3,275 ±254 c	1 ±1	99.9 ±0.1
dry graminoids	2,021 ±140 a	0	100.0 ±0.0	3,402 ±313 b	0	100.0 ±0.0	1,712 ±194 ac	0	100.0 ±0.0	1,371 ±124 c	0 ±0	100.0 ±0.0
green graminoids	1,934 ±141 a	158 ±36 A	90.1 ±2.2 A	783 ±94 b	50 ±14 B	89.7 ±3.6 A	285 ±28 c	14 ±3 B	94.5 ±1.3 A	290 ±26 c	25 ±7 B	90.7 ±2.4 A
total graminoids	3,955 ±277 a	158 ±36 A	95.6 ±1.0 A	4,185 ±363 a	50 ±14 B	98.7 ±0.4 B	1,997 ±214 b	14 ±3 B	99.2 ±0.2 B	1,670 ±141 b	25 ±7 B	98.3 ±0.4 B
dicot, palm and bromelia	958 ±104 a	284 ±219 A	95.9 ±1.3 A	1,430 ±224 a	135 ±34 A	88.9 ±3.4 A	4,547 ±1,270 b	280 ±110 B	89.9 ±3.6 A	2,043 ±220 a	288 ±93 A	90.1 ±2.9 A
WOOD DEBRIS												
0-0.64 cm	-	-	-	-	-	-	295 ±46	26 ±7	89.0 ±2.9 A	288 ±28	53 ±8	78.6 ±3.5 B
0.65-2.54 cm	-	-	-	-	-	-	621 ±75	194 ±44	62.0 ±8.0	572 ±70	229 ±37	53.1 ±7.5
>2.54 cm	-	-	-	-	-	-	829 ±124	400 ±116	41.7 ±9.8	1,001 ±175	543 ±165	39.2 ±9.7
total	-	-	-	-	-	-	1,746 ±162	620 ±134	66.7 ±6.2	1,860 ±206	825 ±167	55.4 ±5.9
SURFACE LAYER												
herb layer+woody debris	5,542 ±322 a	442 ±270 A	91.6 ±5.3 A	7,523 ±548 ab	185 ±41 B	97.1 ±0.7 A	12,099 ±2,039 b	920 ±196 AI	91.6 ±2.5 B	8,838 ±833 ab	1,138 ±206 B	87.2 ±20.5 A
SHURB												
leaf biomass	-	-	-	238 ±45 a	9 ±9	98.5 ±1.5 A	772 ±69 b	93 ±40	89.4 ±3.8 B	390 ±45 c	69 ±22	82.5 ±5.8 B
total biomass	-	-	-	1,690 ±346 a	1,112 ±237 A	26.5 ±5.7 A	6,164 ±555 b	3,918 ±415 B	34.6 ±4.6 A	3,190 ±471 c	2,926 ±441 B	9.6 ±1.3 B
FUEL LOAD	5,542 ±322 a	442 ±270 A	91.6 ±5.3 A	7,761 ±734 b	193 ±39 A	96.7 ±2.9	12,870 ±901 c	1,016 ±1,016 B	91.5 ±2.3	9,229 ±85 b	1,207 ±215 B	87.0 ±2.1
TREE	-	-	-	132 ±91 a	132 ±91 A	0.0	6,584 ±1,749 b	6,584 ±1,749 B	0.0	12,915 ±2,451 c	12,915 ±2,451 C	0.0
TOTAL												
surf.layer+shrub+tree	5,542 ±322 a	442 ±270 A	91.6 ±5.3 A	9,344 ±841 b	1,428 ±125 B	84.3 ±1.2 B	24,847 ±2,459 c	11,422 ±1,242 C	53.7 ±3.7 C	24,944 ±2,943 c	16,979 ±2,648 C	33.0 ±3.4 C
ASH		403 ±10 A			1,283 ±94 B			2,273 ±258 C			1,488 ±171 C	

Different lower case letters denote a significant difference ($P \leq 0.10$) in biomass, when testing between treatments before fire. Different upper case letters denote difference in biomass after fire ($P \leq 0.10$). Different underlined uppercase letters denote a significant difference between combustion factors ($P \leq 0.10$) between treatment. The absence of letters mean no differences were found. Dashes ("-") denote that components were not found in the community.

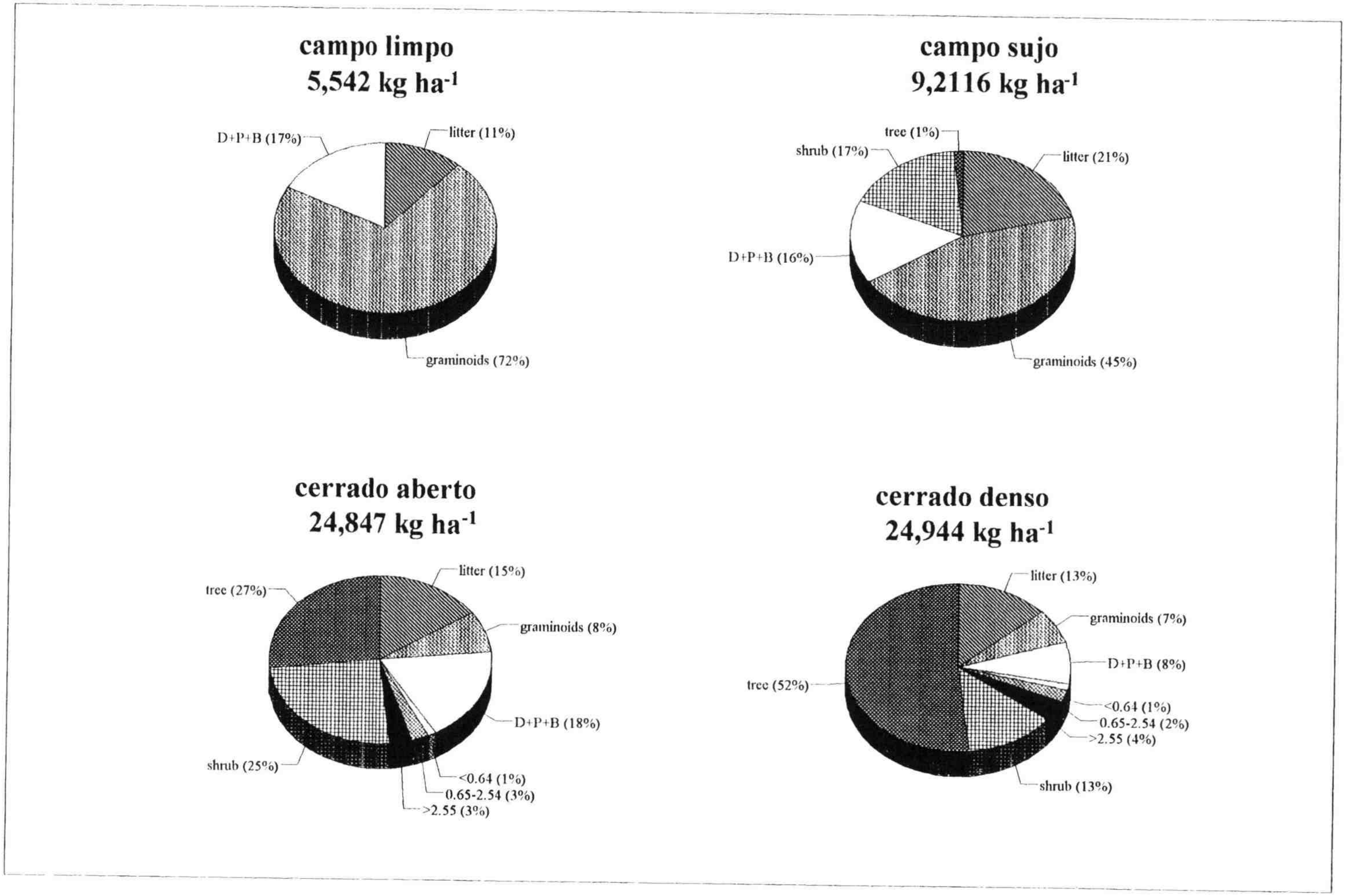


Figure 2.1. Relative proportion of total aboveground biomass components in Cerrado gradient , near Brasilia, DF, Brasil. August-October 1993. D+P+B refers to dicots, bromeliads and palms.

Table 2.2. Shrub (A) and tree (B) density, height and basal area of three community types along a vegetation gradient in Cerrado *sensu lato*. Numbers are mean ± standard

(A)

	campo sujo	cerrado aberto	cerrado denso
SHRUBS			
Density (shrub ha^{-1})	650±80 a	1347±110 b	844±97 c
Height (m)			
mean	0.81±0.34	1.05±0.04	0.93±0.05
range	0.13 - 1.43	0.50 - 1.94	0.55 - 1.77
Basal area/shrub (cm^2)	66.4±14.4	82.6±8.70	74.7±19.1
Basal area/ha ($m^2 ha^{-1}$)	4.3±0.9 a	11.1±1.6 b	6.0±1.3 c

(B)

	campo sujo	cerrado aberto	cerrado denso
TREES			
Density (trees ha^{-1})	28±28 a	1069±124 b	1000±109 b
Height (m)			
mean	2.5±2.5 a	2.92±0.11 b	3.09±0.35 b
range	2.4-2.5	2.01-6.00	2.01-10.00
Basal area/shrub (cm^2)	0.0096±0.0017 a	80.2±12.5 b	145±16.9 c
Basal area/ha ($m^2 ha^{-1}$)	0.0012±0.00083 a	8.5±2.1 b	14.5±2.5 c

Different letters denote a significant difference ($P \leq 0.10$) among communities for both table and (B). The absence of letters mean no differences were found.

Fuel load, defined as the portion of aboveground biomass susceptible to fire (e.g. surface layer plus shrub leaves) (Kauffman et al. 1994), in campo limpo was the same as TAGB. Fuel load significantly increased from campo sujo to cerrado aberto and decreased in cerrado denso (Table 2.1.).

Fire behavior

Weather conditions were similar at the time of burning for all communities, except for campo limpo, which had higher wind speeds (8-10 km h^{-1}). Ambient temperatures ranged from 27 °C to 32 °C, and relative humidity averaged 36 % (Table 2.3.).

Mean moisture content of graminoids, the dominant component responsible for sustained ignition and spread, was very high in campo limpo (52.7 %), while campo sujo had the lowest moisture content (8.9 %). Wood debris and litter were the components with the lowest moisture content in cerrado aberto and cerrado denso (Table 2.3.).

Fire behavior in each community differed. Flame length ranged from 1.4 m to 3.4 m. Flame height and fireline intensity increased from campo limpo (557 kW m^{-1}) to cerrado denso (3,693 kW m^{-1}). Reaction intensity increased from campo limpo to cerrado denso (506 to 1,319 kW m^{-1}) (Table 2.4.).

Consumption

The combustion factor, defined as the percent of biomass consumed by fire, was 91 % and 84 % for campo limpo and campo sujo, respectively. In both campo limpo and campo sujo, litter and dormant grass were completely consumed by fire with small

Table 2.3. Weather conditions and fuel moisture content (%) at the time of prescribed burning along a vegetation gradient of Cerrado *sensu lato* , near Brasilia, DF, Brazil. Data are means ± standard error.

	campo limpo	campo sujo	cerrado aberto	cerrado denso
DATE OF BURNING	7 October 1993	17 August 1993	30 August 1993	31 August 1993
WEATHER CONDITIONS				
Temperature (°C)	27	27	32	30
Relative humidity (%)	40	37	35	31
Wind speed (km/h)	5-6	N/A	0-5	0-3
Wind direction	S-N	S-W	N	N
General conditions	cloudy	clear	-	hazy, partly cloudy
FUEL MOISTURE CONTENT (% dry weight basis)				
graminoids	52.70±3.11	8.93±1.14	26.85±6.96	24.46±4.73
dicot	114.33±11.75	113.47±8.26	110.89±4.31	136.69±5.20
woody debris	-	-	4.87±1.51	6.04±1.03
litter	-	-	4.75±0.25	5.44±0.97
soil	32.97±0.86	33.06±1.31	19.95±1.95	18.02±0.80

Dash ("-") means that component was not present in that community. N/A means that data was not collected.

Table 2.4. Fire behavior along a vegetation gradient of Cerrado, near Brasilia, DF, Brazil. Data are means ± standard error.

	campo limpo	campo sujo	cerrado aberto	cerrado denso
Flame length (m)	1.4±0.2	2.8±0.5	3.1+0.4	3.4±0.3
Flame height (m)	1.2±0.2	2.2±0.5	2.7±0.3	2.9±0.4
Flame depth (m)	1.1±0.3	3.0±2.0	3.8±0.4	2.8±0.3
Flame angle (degree)	52.5±7.1	45.0±0	63.2±4.3	61.8±6.4
Rate of spread(m/min)	2.0±1.0	N/A	13.8±2.4	13.8±(0.3
Residense time (s)	2.0±1.0	N/A	31.6±1.8	28.5±6.8
Fire line intenity (kW/m)	556.9	2436.8	3093.8	3692.7
Reaction intensiy (kW/m^2)	506.3	812.3	814.2	1318.8
Heat per unit area (kJ/m^2)	278.5	-	224.2	267.7

N/A means that measurements were not taken. Statistics were not applied because sample sizes were too small.

amounts of green grass and dicots remaining after fire in both communities. The combustion factor of dormant grassland and litter components in cerrado aberto and cerrado denso was 100 % and 99 %, respectively. Higher consumption rates were measured for smaller diameter classes of wood debris. Consumption of woody debris was > 82 % in all communities. In campo sujo, shrub leaves had the highest combustion factor (98%), and was significantly different from cerrado aberto and cerrado denso. Considering total shrub biomass (stem and leaves) cerrado aberto had the highest consumption (35 %). Fuel loads consumption was high for all communities (>87 %), and differences were not detected among communities (Table 2.1.).

Post-fire biomass

After fire, TAGB of campo limpo and campo sujo differed significantly between themselves and from cerrado aberto which in turn was different from cerrado denso (Table 2.1.). Shrub stems and trees comprised the dominant biomass component in cerrado aberto and cerrado denso after fire.

Fuel load was found in small amounts after fire. In campo sujo, it declined to 193 kg ha^{-1}, while cerrado aberto had 1,016 kg ha^{-1}, and cerrado denso had 1,207 kg ha^{-1}. Ash mass had greatest quantity in cerrado aberto and cerrado denso, while ash mass in campo limpo was the lowest (Table 2.1.).

Discussion

Pre-fire biomass

The Brazilian Cerrado s.l. comprises a variety of vegetation communities, each with a unique composition, and structure (Eiten 1972). This variable community structure, ranging from a grassland (campo limpo) to woodland (cerrado denso), results in differences in biomass of components, fuel load, and TABG within each community type. Kauffman et al. (1994) reported a fuel load of 7,128 kg ha^{-1} for campo limpo, 7,321 kg ha^{-1} for campo sujo; 8,625 kg ha^{-1} for campo cerrado, and 10,031 kg ha^{-1} for cerrado *sensu stricto*. In my study, campo sujo had a similar fuel load, while campo limpo had lower fuel load. Cerrado aberto and cerrado denso fuel load was little higher than fuel loads in campo cerrado and cerrado *sensu stricto* found by Kauffman et al. (1994) Although, the same area was studied, yearly variation in productivity may occur due to different environmental conditions.

In this study, TABG increased as the shrubs and trees increased along the Cerrado gradient. The TABG for cerrado denso (24,944 kg ha^{-1}), which was the highest among the four communities, was quite low compared to other Brazilian forest ecosystems. For example, TABG of Caatinga, a tropical dry forest, is 74 Mg ha^{-1} (Kauffman et al.1993). TABG of Amazonian tropical rain forest is estimated from forest inventory data to be 263 Mg ha^{-1} and 252 Mg ha^{-1} for Para and Rondonia states respectively (Brown and Lugo 1992). Direct measurements, including trees < 0.10 m in diameter at breast height, palms, dead coarse wood debris, in a primary slashed forest is reported to range from 290 to 435 Mg ha^{-1} in the states of Rondonia and Para (Kauffman et al 1995). Comparative estimates of TABG for Cerrado s.l. are scarce. Based upon fuel wood inventories, Fearnside (1992) estimated TABG for Cerrado to range from 11 to 52 Mg ha^{-1}. Although biomass estimated here for cerrado aberto and cerrado denso is within the range proposed by Fearnside (1992), both must be viewed with caution, given shortcomings in biomass estimation techniques. In my study, tree biomass was calculated from regression equations developed for tropical moist forest. Given differences in structures between Cerrado and moist forest, the degree of error in estimation is unknown (Brown et al. 1989).

Studies that partition and describe TABG into components are rare for Cerrado s.l. (Kauffman et al. 1994). Among vegetation communities in this study, a great variability in biomass ecosystem components existed. For example, cerrado aberto and cerrado denso had a similar TABG; however, the biomass of shrubs and trees differed. The biomass of the graminoids and herbaceous layer decreased with the occurrence of shrubs and trees. This decrease in the live understory vegetation may be less affected by soil moisture or nutrient competition than by light, limiting competition with the overstory (Coutinho 1978b). Although there is a decrease, an herbaceous layer still existed in the denser tree community studied here (cerrado denso). Cerrado trees typically have large and few leaves especially when compared with tropical moist forest trees. This results in less light attenuation by the overstory tree canopy, thereby allowing a herbaceous layer to develop (Eiten 1972). Conversely, litter increased along the gradient from campo limpo to cerrado denso as a consequence of increasing shrub and tree biomass. Wood debris were present in the communities where occurrence of shrubs and trees were abundant.

Fire behavior

Fire had both short- and long term effects on the ecosystem (Muraro 1971 cited in Alexander 1982). The immediate physical effects include the consumption of aboveground biomass and ash deposition. Long term effects may include influences on nutrient pools and cycles within the ecosystem. Nutrient balances are influenced by the incorporation of nutrients from the ash to the soil as well as inputs from precipitation and dry fall (Coutinho 1979, Pivello and Coutinho 1992, Kauffman et al. 1994). The arrangement and quantity of each component found in this study likely influences the flammability and fire behavior of this ecosystem. The fire behavior influence on vegetation composition and structure is related to, and dependent upon the fuel consumption, weather conditions at the time of burning, topography, and fuel moisture content (Chandler et al. 1983, Pyne 1984). Weather conditions were similar for campo sujo, cerrado aberto and cerrado denso. Therefore, differences in fire behavior for these communities are probably due to differences in fuel bed structure, arrangement, quantity and the fuel moisture content. Grass fires potentially have the most rapid rate of spread of all natural fuels (Chandler et al. 1983). This is particularly true when grasses are dry and in a continuous arrangement (Brown and Davis 1973), as was found in campo sujo. Campo sujo was burnt at the end of the dry season; only a slight rain event occurred three days before fire. This likely contributes for the very low moisture content in the graminoids component (8.9 %). Since graminoids comprised 46 % of this community, such low moisture content was responsible for the sustained ignition and spread of fire. Although the rate of spread was not recorded, I suspect that it was very fast because an area of 10 ha burnt in 11 min. With the increase of shrubs and trees in cerrado aberto and cerrado denso, the rate of spread was expected to decline because of changes in fuel composition (decreases in grasses, increases in live fuels and litter). In addition, the occurrence of a vertical structure likely influenced the microclimate; lower in-stand wind speeds, and higher relative humidity in the understory may influence fire behavior. Conversely, campo limpo was burnt after a series of successive rains in the weeks before the fire. In addition, because of a high wind speeds, it was necessary to use a backfire ignition pattern in campo limpo. This dramatically lowered flame lengths and rate of spread compared to the other communities.

Fireline intensity is used to classify fires and facilitate comparisons of behavior between fires (Alexander 1982). Campo cerrado and cerrado s.s. have been recorded to have 2,842 kW m^{-1} and 3,455 kW m^{-1}, respectively (Kauffman et al. 1994). These are in the range of the energy released in cerrado aberto (3,194 kW m^{-1}) and cerrado denso (3,693 kW m^{-1}) in this study. Fireline intensity is related positively with flaming length, which in turn is responsible for tree scorch height and crown mortality (Van Wagner 1973). Although trees in Cerrado s.l. are well adapted to fire, it was observed that some tree leave, which escaped from fire, lost their leaves due to lethal scorch temperature. Ramos (1990) reported that fire resulted in leaf loss of shrubs that were not consumed by fire. Flame length in campo limpo (1.4 m) and in campo sujo (2.8 m) fell in the range reported for African grassland (Trollope 1978); a backfire technique resulted in 0.5-1.5 m, while flames heading wind had a mean of 2.8 m. Heat per unit area is used to measure the heat the surface, and results may influence future soil environment (Rothermel and Deeming 1980). Although soil far below the surface is not affected by the high temperature, heating of the surface ground may increase nitrogen mineralization, microbial activity, and pH (Kauffman et al. 1992). Consequently, heat per unit area may influence nutrient availability for plant recovering of determined area. Reaction intensity for campo sujo (812 kW m^{-2}) and cerrado aberto (814 kW m^{-2}) were similar. However, it is unlikely that fire effects for these two community types would be similar, because fireline intensity and depth were different. Parameters such as fireline intensity, heat per area, and reaction intensity must be interpreted together, considering yet rate of spread to have an acceptable description of fire behavior (Alexander 1982).

Consumption and post-fire biomass

In campo limpo and campo sujo almost all of the aboveground biomass was consumed because composition of these communities was predominantly highly flammable grasses. Grasses were in a continuous horizontal layer that facilitated an efficient spread of fire through the ecosystem. The lower combustion factor in the cerrado aberto and denso was related to a less efficient combustion of wood debris, shrub branches, and trees that were either partially burned or unburned in the area after fire. Although consumption of the herbaceous layer and shrub leave was high in my study, complete mortality of vegetation in cerrado is extremely rare when under a natural fire-return interval. (Ramos 1990). Ramos did not find any differences in mortality of individual shrubs and trees when comparing an area of Cerrado protected from fire with an area of biennial burns.

Among Brazilian ecosystems, Cerrado vegetation, especially woodland communities, has the lowest consumption (53 % in cerrado aberto, 33% in cerrado denso). In contrast, Caatinga, a tropical dry forest in Northern of Brazil ranged from 77 to 89 % of aboveground consumption, depending on the season of burning (Kauffman et al. 1993). Slashed primary forest accounted for consumption of between 42 and 57 %. (Kauffman et al. 1994). Consumption of slashed second growth tropical forest is probably higher because its structure is lower. Since plant biomass consumption results in CO_2 release to atmosphere, individual fires in Cerrado vegetation do not cause much of an immediate increasing of CO_2 in the atmosphere compared with other tropical ecosystems.

Ash mass appeared to be related to pre-fire fuel biomass, and hence consumption. The variability of ash composition also depended upon the pre-fire fuel biomass. Fine particles found in campo limpo and campo sujo ash were a consequence of the high consumption of graminoid material. Cerrado aberto and cerrado denso ash was composed of fragments of charcoal, burned twigs and leaves. Smoldering combustion observed in cerrado aberto was principally in wood debris > 2.54 cm in diameter. It is expected that a portion of the ash (mineralized nutrients) is incorporate into the soil while some is lost via the wind and water to adjacent areas.

Conclusion

Total aboveground biomass and composition in the Cerrado s.l. near Brasilia, Brazil, varied along a vegetation gradient of increasing wood structure. The grasslands, campo limpo and campo sujo had little, if any, shrubs and trees; consequently, their total aboveground biomass was lower than that of cerrado aberto and cerrado denso. This composition and arrangement combined with moisture content and weather conditions appeared to influence fire behavior in Cerrado s.l..

Fire plays a dominant ecological function in this ecosystem, and it is important in shaping the different communities. Descriptions of fire behavior were different for each community type. In this study, fireline intensity was lower for grassland than for wood communities.

Total biomass of Cerrado s.l. in this study was found to be the lowest mass among tropical forests in Brazil. As vegetation is a source and sink of C, combustion results in the release of these stored C and mineral nutrients. Consequently, the contribution of the Cerrado s.l. to the increase of CO_2 and to the greenhouse effect is probably the lower on the basis of area than that of other Brazilian ecosystems. Moreover, Cerrado vegetation recovers rapidly after fire resulting in C uptake to pre-fire levels in one to two years. These combined with the well-adapted morphological and reproductive traits of Cerrado vegetation may indicate fire as a natural disturbance in this ecosystem.

To understand the fire ecology of Cerrado vegetation, it is essential to learn its function, dynamics, nature and variability. Fire may enhance habitats by creating seed beds, controlling diseases and pests, and reducing a wild fire hazard. However, this will vary by vegetation community type resulting in even a higher level of diversity.

Reference

Ab'Saber, A. N. 1983. O domínio dos cerrados: introdução ao conhecimento. Revista do Servidor Publico 111(4):41-55.

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:349-357.

Alho, C. J. R. 1990. Distribuição da fauna num gradiente de recursos em mosaico. Paginas 205-356 in M. N. Pinto, editor. Cerrado: Caracterização, Ocupação e Pespectivas, Primeira Edição. Editora da UnB, Brasilia, DF.

Batmanian, G. J. 1983. Efeitos do fogo sobre a produção primária e a acumulação de nutrientes no estrato rasteiro de um cerrado. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Berger, R., and W. F. Libby. 1966. UCLA Radiocarbon Dates V. Radiocarbon 8:467-497.

Brown, A. A., and K. P. Davis. 1973. Forest Fire: Control and Use. Mcgraw-Hill Company, New York.

Brown, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. Forest Science 17(1):96-102.

Brown, J. K., and P. J. Roussopoulos. 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. Forest Science 14:350-356.

Brown, S., and A. E. Lugo. 1993. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8-18.

Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with application to forest inventory data. Forest Science 35(4):881-902.

Cavalcanti, L. H. 1978. Efeito das cinzas resultantes da queimada sobre a produtividade do estrato herbaceo subarbustivo do cerrado de Emas. Tese de Livre Docencia. Universidade de São Paulo, São Paulo.

Cesar, H. L. 1980. Efeitos da queima e corte sobre a vegetação de um campo sujo na fazenda Água Limpa, Distrito Federal. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Chandler, C., P. Cheney, P. Thomas, L. Trabaud, and D. Williams. 1983. Fire in the Forest - Forest Behavior and Effects. Volume 1. John Wiley & Sons, New York.

Coutinho, L. M. 1976. Contribuição ao conhecimento do papel ecológico das queimadas na floração de especies do cerrado. Livre Docente Tese. Universidade de São Paulo, São Paulo, SP.

Coutinho, L. M. 1978b. O conceito de cerrado. Revista Brasileira de Botânica 1:17-23.

Coutinho, L. M. 1979. Aspectos ecológicos do fogo no cerrado. III - A precipitação atmosférica de nutrientes minerais. Revista Brasileira de Botânica 2:97-101.

Coutinho, L. M. 1981. Aspectos ecológicos do fogo no cerrado - Nota sobre a ocorrência e datação de carvões vegetatis encontrados no interior do solo, em Emas, Pirassununga,SP. Revista Brasileira de Botânica 4:115-117.

Coutinho, L. M. 1982. Ecological effects of fire in Brazilian cerrados. Pages 273-291 in B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savannas. Volume 42. Springer-Verlag, Berlin.

Coutinho, L. M. 1990. Fire in the ecology of the Brazilian cerrado. Pages 82-105 in J. G. Goldammer, editor. Fire in the Tropical Biota- Ecosystem Process and Global Challenges. Volume 84. Springer Berlag, Berlin.

Deeming, J. E., R. E. Burgan, and J. D. Cohen. 1977. The National fire danger rating system. USDA Forest Service General Technical Report INT-39.Ogden,UT.

DNER-Departamento Nacional de Estradas de Rodagem. 1976. Classificação climatica de Wladimdir Koppen, Reimpressão. Servico de Publicação, Rio de Janeiro.

Eiten, G. 1972. The cerrado vegetation of Brazil. Botanical Review 38:201-341.

Eiten, G.. 1975. Vegetation of the Serra do Roncador. Biotropica 7:112-135.

Fearnside, P. M. 1992. Greenhouse gas emissions from deforastation in the Brazilian Amazon. in W. Makundi and J. Sathaye, editors. Carbon emissions and sequestration in forests: case studies from seven developing countries, Draft Edition. Volume 2. U.S. Environmental protection Agency, Climate Change Division, Washington, DC and Energy and Environment Division,Lawrence Berkeley Laboratory, Berkeley, CA, .

Felfili, J and Silva Jr. 1993. A comparative study of cerrado (sensu stricto) vegetation in Central Brazil. Journal of Tropical Ecology 9:227-289.

Furley, P. A., and J. A. Ratter. 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. Journal of Biogeography 15:97-108

Goedert, W. J. 1983. Managemnet of the Cerrado soils of Brazil: a review. Journal of Soil Science 34:405-428.

Goodland, R., and Pollard. 1973. The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology 61:219-224.

Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. Journal of Ecology 82:519-531.

Kaufffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: Biomass, nutrient pools, and losses in slashed primary forests. in press.

Kauffman, J. B., R. L. Sanford Jr., D. L. Cummings, I. H. Salcedo, and E. V. S. B. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74(1):140-151.

Kauffman, J. B., K. M. Till, and R. W. Shea. 1992. Biogeochemistry of deforastation and biomass burning. Pages 426-456 in D. A. Dunnette and R. J. O'Brien, editors. The Science of Global Change: The impact of human activities on the Environment, Americal Chemical Society Symposium Edition. Volume Series 483. American Chemnical Society, Washington,DC.

Klinge, H., W. A. Rodrigues, E. Brunig, and E. J. Fittkau. 1975. Biomass and structure in a central Amazonian rain forest. Pages 398 in F. B. Golley and E. Medina, editors. Tropical Ecological Systems - Trends in Terrestrial and Aquatic Research. Volume Ecological Studies 11. Springer-Verlag, New York.

Magalhães, J. V. C. de. 1913. O Selvagem, Segunda Edição. Editora Livraria Itatiaia e Editora da Universidade de São Paulo, São Paulo.

Pivello, V. R., and L. M. Coutinho. 1992. Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). Journal of Tropical Ecology 8:487-497.

Pyne, S. J. 1984. Introduction to Wildland Fire: Fire Management in the United States, 1st Edition. John Wiley & Sons, New York,NW.

Rachid-Edwards, M. 1956. Alguns dispositivos para proteção de plantas contra a seca e o fogo. Boletim da Faculdade de Filosofia, Ciências e Letras da USP Botânica 13:37-69.

Ramos, A. E. 1990. Efeitos da queima sobre a vegetação lenhosa do cerrado. Tese de Mestrado. Universidade de Brasilia (Brasilia, DF).

Rosa, C. M. M. 1990. Recuperação pos fogo do estrato rasteiro de um campo sujo de cerrado. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Rothermel, R. C., and J. E. Deeming. 1980. Measuring and interpreting fire behavior for correlation with fire effects. USDA-For. Serv. Gen. Tech. Rep.INT-93, Ogden,UT.

Sambuichi, R. H. R. 1991. Efeitos de longo prazo do fogo periódico sobre a fitossociologia da camada lenhosa de um Cerrado em Brasilia, DF. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Sarmiento, G. 1983. The savannas of tropical America. Pages 245-288 in F. Bourlière, editor. Tropical Savannas. Volume Ecosystems of the World - 13. Elsevier, Amsterdan.

Silberbauer-Gottsberger I. and Eiten G. 1987. A hectare of Cerrado. I. General aspects of the trees and thick-stemmed shrubs. Phyton 27(1):55-91.

Trollope, Q. S. W. 1978. Fire Behavior - a preliminary study. Proceedings of the Grassland Society of Southern Africa 13:123-128.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, second Edition. W, H, Freeman and Company, New York.

Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. Forest Science 14(1):20-26.

Van Wagner, C. E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research 3:373-378

CHAPTER 3
ROOT BIOMASS IN CERRADO VEGETATION NEAR BRASILIA, BRAZIL

Abstract

Deforestation and conversion to agriculture is occurring in vast areas in the Cerrado *sensu lato* (a tropical savanna ranging from pure grasslands to woodlands), yet few studies have quantified total biomass or nutrient pools in this ecosystem. Root biomass was quantified along this gradient in four plant communities at the Instituto Brasileiro de Geografia e Estatística (IBGE) Ecological Reserve, and the Jardim Botânico de Brasilia (JBB) Ecological Reserve, both in Brasilia, DF, Brazil.

Root biomass increased from the pure grassland, campo limpo (16,317 kg ha^{-1}) to woodland, cerrado denso (52,907 kg ha^{-1}). The proportion of the total root biomass in the upper 20 cm of soil was 63 % for campo limpo, 73 % for campo sujo, 79 % for cerrado aberto and 62 % for cerrado denso. More than 80 % of root biomass occurred in the upper 30 cm of the soil, except for cerrado denso (71 %).

Fine roots ($\leq$ 0.5 cm in diameter) dominated in grasslands and decreased in the woodlands. In campo limpo, fine roots were 56 % of its total root biomass, campo sujo was 46 %, cerrado aberto was 40 % and cerrado denso was 29 %. Nevertheless, coarse root class diameter ($\geq$ 0.6 cm in diameter) increased from campo limpo to cerrado denso.

Root:shoot ratio in communities was very high indicating that more than 71 % of its live phytomass (aboveground biomass + root biomass) is in the belowground. These results were unique for tropical ecosystems. Root:shoot ratios in the Cerrado *sensu lato* were among the highest for tropical ecosystems. This is likely related to survival strategies associated with frequent fires and severe dry seasons typical of this ecosystem. These belowground pools may be significant sources of carbon (C) pools when Cerrado *sensu lato* is converted to agriculture.

Introduction

In most ecosystems of the world roots have not received the same level of study as aerial parts of plants (Russel 1977, Sanford 1989). This lack of attention is related to the time consuming methods associated with excavations, and to the necessity of disturbance in the study area (Santantonio et al. 1977). Functions of roots and belowground tissues include uptake and storage of water and nutrients (Jesko 1992). Roots are significant sink of the carbon (C) fixed by aboveground tissues. For example, in a temperate deciduous (*Liriodendron*) forest, 45 % of all C fixed is used in the production of root biomass and root respiration (Harris et al. 1972). Since roots are part of the ecosystem, a better knowledge of their biomass and distribution is important to understand C dynamics of the whole ecosystem. Issues of the relationship between increasing atmospheric CO_2 and climate change, and accelerated levels of tropical deforestation require better quantification of the total aboveground and belowground biomass pools (Fearnside 1992).

Root biomass has been quantified in few neotropical ecosystems. In the tropical dry forest, total root biomass has been estimated to range from 31 to 45 Mg ha^{-1} (Murphy and Lugo 1986, Castellanos et al. 1991). In the Venezuelan Amazon tropical rain forests, Sanford (1989) reported root biomass ranges from 54.6 to 60.9 Mg ha^{-1} in three different forest community types. In Brazil, Para state, Nepstad (1989), compared root distribution in an intact tropical rain forest and a grass/shrub vegetation, finding 35.4 and 9.7 Mg ha^{-1} respectively.

A gradient of grassland to woodland known as Cerrado *sensu lato* comprises 23 % of Brazil area. Like tropical savannas, it evolved with a history frequent fire under a nutrient poor soils and in a climate with marked wet and dry seasons.

In Cerrado s.l., root systems of individual species were classified as deep-rooted, shallow-rooted and medium-rooted (Rawitscher 1948). Rachid-Edwards (1956) described underground adaptations to drought and fire for selected species of the Poaceae family. Descriptions of subterranean organs and their potential of vegetation reproduction were discussed by Rizzini and Heringer (1961, 1962). However, total root biomass in this ecosystem has not been investigated. I hypothesized that among adaptations to frequent fire, annual drought, and poor soil nutrients, a greater portion of resources would be sent to the belowground system, so that root biomass and root:shoot ratios would be high relative to other tropical ecosystems.

The objectives of this study were to (a) quantify and compare the total root biomass along four communities types varying from grasslands to woodlands, (b) quantify the vertical root distribution down to soil depth of 2.00 m for each community type, (c) quantify the diameter size distribution of roots, and (d) compare root biomass with total aboveground biomass data and describe root:shoot ratio for communities along this Cerrado gradient.

Study Site

Research was conducted at the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE Ecological Reserve) and the Jardim Botânico de Brasilia (JBB Ecological Reserve). These sites are located about 35 km south of Brasilia, in Brazil (15^{o} 51' S 47^{o} 63' W). The elevation is 1,100 m and slopes are < 10%. From 1980 to 1992, mean annual temperature varied from 19.2 °C to 22.4 °C. Mean precipitation was 1482 mm distributed in two distinctive seasons: a wet season from October to March with 1257 mm and the dry season from April to September with

225 mm. Mean maximum relative humidity was 81% in December and the mean minimum was 55% in August (File data from Estação Agroclimatológica do IBGE 1980-1992).

Soil in these areas are poor in nutrient concentration, with high aluminum content, and high pH. Vegetation is characterized by the five community types described for Cerrado s.l., i.e. campo limpo (grassland), campo sujo (grassland with scarce shrubs), campo cerrado (dominance of shrubs with scattered trees and some grasses), cerrado *sensu stricto* (s.s) (dominance of trees with scattered shrubs and some grasses), and cerradão (a closed canopy forest) (Eiten 1972, Coutinho 1978b, Goodland and Pollard (1973). Moreover, within cerrado s.s., areas with a more open tree canopy are referred here as cerrado aberto and those with a more closed canopy as cerrado denso variations with a more open(cerrado aberto) and closed tree canopy (cerrado denso) than cerrado *s.s.* is also found. In this study, root biomass was investigated in campo limpo, campo sujo and in the two variants of cerrado s.s.: cerrado aberto and cerrado denso.

Methods

Root biomass was quantified by a combination of monolith and auger methods (Böhn 1979). A trench was dug prior to root excavation and at the top of one side wall, an area of 0.50 x 0.50 m was marked and all aboveground vegetation was clipped and removed. From this side wall, into this area, roots within this monolith were excavated by layers (0-10 cm, 10-20 cm, 20-30 cm, 30-50 cm and 50-100 cm). From 100 cm to 200 cm an auger of 15 cm in diameter was used. Five samples (five holes) per community type were systematically selected and measured.

All material (soil and roots) was sieved in the field. Roots were taken to the laboratory, and dried at 60 °C for 48 hours. Later, roots were separated into five classes according to diameter: ≤0.5 cm, 0.6-1.0 cm, 1.1-2.0 cm, 2.1-3.0 cm, and tubers. Tubers included all other root structures found in Cerrado s.l., such as tubercle roots, xylopodia, lignotubers and rhizome. Finally, the material was weighed.

The study was established in a systematic design. In a linear arrangement five holes were dug approximately 20 m apart. While most samples had a normal distribution, homogeneity of variances did not occur (Barlett's test, p-value ≥ 0.10). Therefore, a non-parametric Kruskal-Wallis test was applied to test for differences among root biomass of community types (p-value = 0.10). If significant, a Mann-Whitney test was applied to separate the treatments (Sokal and Rohlf 1981). Medians and means were similar, indicating that samples differed in variance yet were normally distributed, therefore, means are used in the text, tables and graphics.

Results

Total root biomass in the Cerrado gradient, near Brasilia, Brazil, increased from the campo limpo (grassland) to cerrado denso(woodland). Total root biomass for campo limpo and campo sujo were significantly different from cerrado aberto and cerrado denso (Table 3.1.).

Distribution of root biomass by depth for each community was similar with root biomass tending to decrease with soil depth. This decrease was most dramatic in campo limpo, the community without woody vegetation (Figure 3.1.).

Along the vegetation gradient from grassland to woodland, the relative concentration of roots in the top 10 cm was approximately 50 % for campo limpo, campo sujo, and cerrado aberto, and 31 % for cerrado denso. In contrast at a depth of 10-20 cm, the proportion of root biomass increased from campo limpo (10 %) to cerrado denso (31 %).

Table 3.1. Total root biomass (kg ha^{-1}) along the Cerrado *sensu lato* in Brasilia, DF, Brazil.

communities	Root biomass		
	mean ± SE		median ± QD
campo limpo	16,317 ±2,519	a	16,274 ±1,534
campo sujo	30,083 ±4,594	a	30,270 ±6,516
cerrado aberto	46,584 ±6,135	b	41,938 ±3,775
cerrado denso	52,908 ±8,429	b	49,713 ±15,986

Different letters denote significant differences (p-value < 0.10) in biomass when testing between communities using Mann-Whitney test. Means are followed by standard error, and medians are followed by quartile deviation (N=5). The rough similarity between means and medians indicate that root biomass distribution was not too skewed.

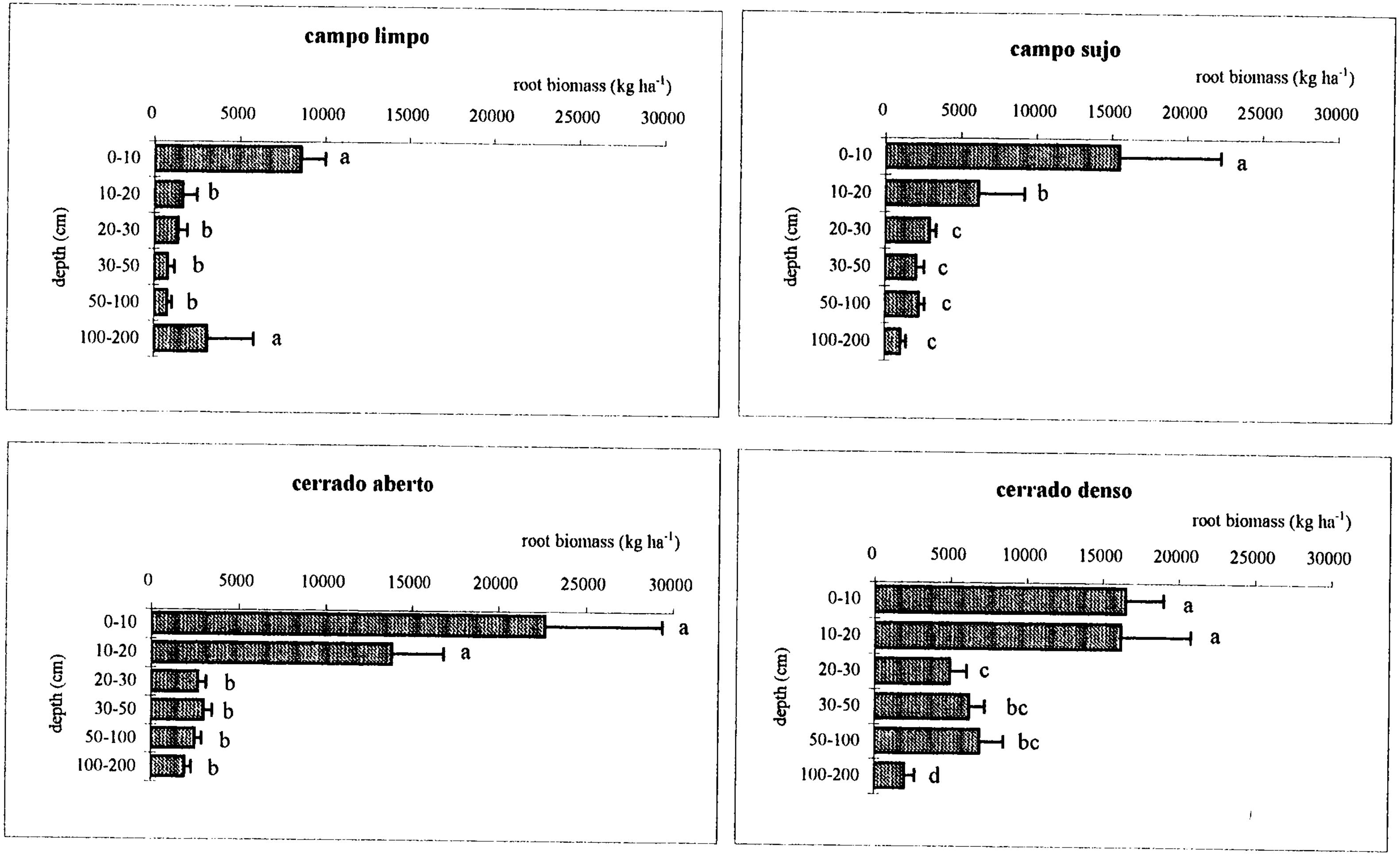


Figure 3.1. Root biomass distribution by depth in Cerrado *sensu lato*, near Brasilia, Brazil. Different letters refer to significant differences in biomass by depth within each community (p-value = 0.10).

Most of the roots were concentrated in the first 20 cm in depth for all communities; campo limpo had 63%, campo sujo 73 %, cerrado aberto 79 %, and cerrado denso 62 %. In cerrado denso, 71 % of the total root biomass was found in the upper 30 cm of soil. In all other communities it was more than 80 %. Roots in the 30-50 cm soil depth comprised 5 to 12 % of the total root biomass. At depths of 50-100 cm, roots comprised 5 to 13 % of the total pool. Only 3 to 4 % of the total pool was at a depth of 100-200 cm except in campo limpo, which had 19 % of its total root at this depth.1

Roots ≤ 0.5 cm in diameter were the dominant diameter class in term of biomass along this Cerrado gradient. While biomass of fine roots increased along the cerrado vegetation gradient, the relative contribution decreased. In campo limpo, campo sujo, cerrado aberto and cerrado denso roots ≤ 0.5 cm comprised 56 %, 46 %, 40% and 29 % their respective total root biomass. In contrast, the relative abundance of coarse roots (diameter classes ≥ 0.6 cm), increased from campo limpo to cerrado denso. Coarse root biomass was 7,146 kg/ha (44 %) in campo limpo, 16,275 kg ha^{-1} (54 %) in campo sujo, 27,954 kg ha^{-1} (60 %) in cerrado aberto; 37,518 kg ha^{-1} (71 %) in cerrado denso (Figure 3.2.). Tubers were present in all communities (Figure 3.2.) comprising 9 % in campo sujo to 23% in cerrado aberto.

The difference in total root biomass between community types in Cerrado s.l. was also found for total aboveground biomass for this same study area (Chapter 2). Total ecosystem phytomass (live aboveground biomass and root biomass) in Cerrado gradient varied from 19,209 kg ha^{-1} for campo limpo to 71,345 kg ha^{-1} for cerrado denso (Table 3.2.). Campo sujo had the highest root:shoot ratio with 7.7; and cerrado aberto had the lowest ratio, 2.6 (Table 3.2.).

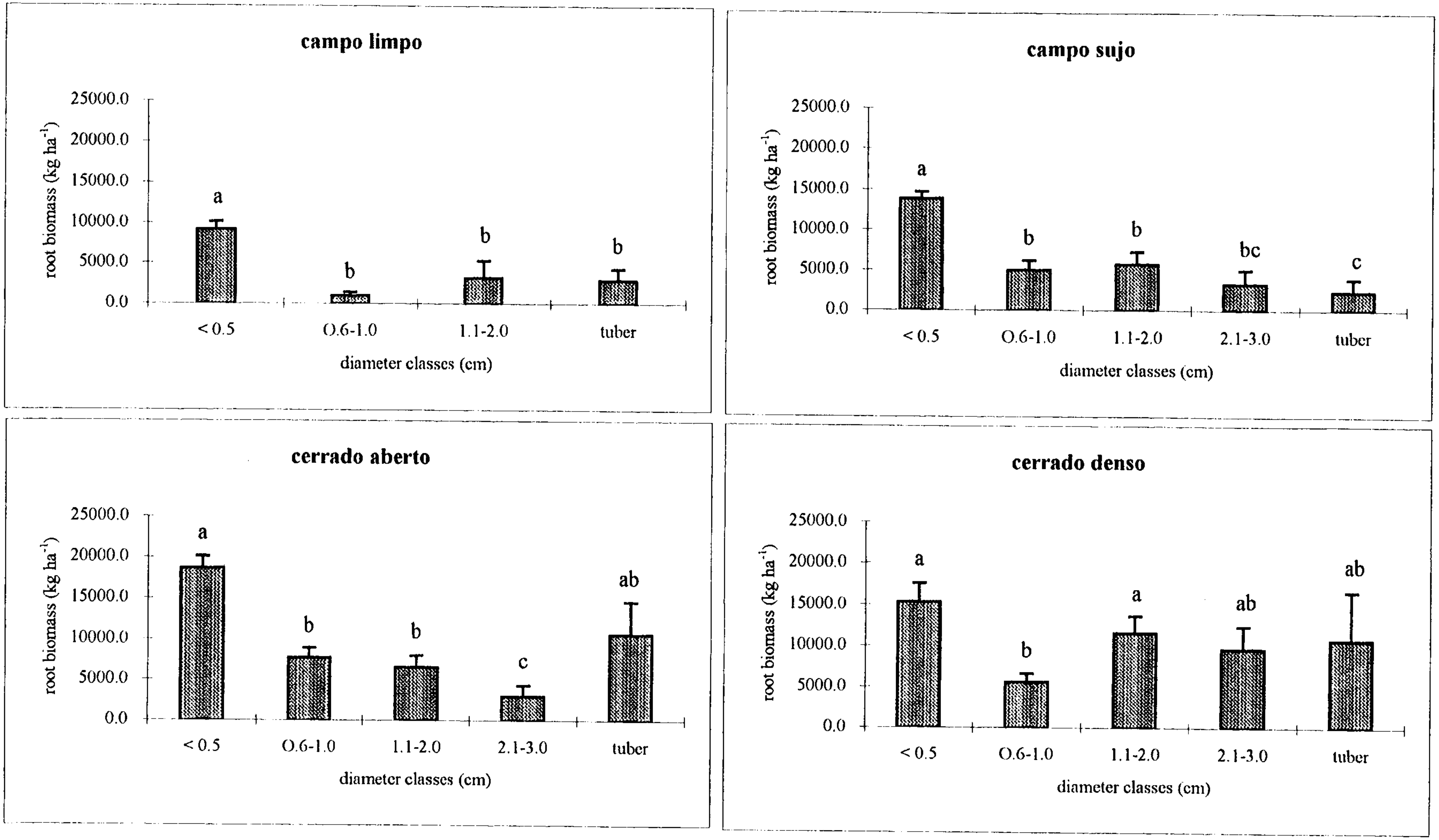


Figure 3.2. Root biomass by diameter in Cerrado gradient, near Brasilia, Brazil. In campo limpo, roots with diameter between 2.1-3.0 cm were absent. Different letters refer to a significant differences in biomass by diameter and tuber within each

Table 3.2. Total phytomass (kg ha^{-1}) of the Cerrado *sensu lato*, near Brasilia,DF, Brazil.

live biomass	campo limpo	campo sujo	cerrado aberto	cerrado denso
green grass	1,934	783	285	290
dicot+palm+bromelia	958	1,430	4,547	2,043
shrub	-	1,690	6,164	3,190
tree	-	132	6,584	12,915
aboveground (shoot)	2,892	4,035	17,580	18,438
belowground (root)	16,317	30,083	46,584	54,908
total phytomass	19,209	34,118	64,164	73,345
root:shoot	5.6	7.7	2.6	2.9

Discussion

The structure and biomass of root systems are related to the species' genetic inheritance and to environmental factors of the ecosystem (Kerfoot 1963, and Richards 1986). Environmental factors affecting root structure and biomass include soil related to soil moisture, macronutrient availability as well as soil physical characteristics (Rizzini and Heringer 1961, Richards 1986). Goodland and Pollard (1973) studied variability in soil chemistry along the Cerrado s.l. as a factor influencing vegetation structure from campo sujo to cerradão (Goodland & Pollard 1973). They found higher nutrient concentration in the soil for community types with greater tree density and basal area. Askew et al. (1971) investigated the soil moisture content along a transect from grassland to woodland in Cerrado s.l. area of Mato Grosso state, Brazil. Soil moisture content up to 1.05 m in depth was higher for grassland than for woodland during the entire year. Soil classification and a brief association of community vegetation types were described by Haridasan (1990). Most of the cerrado s.s., campo cerrado and campo sujo are related to Latosols (Oxisols) and Podzolic (Afsols or Ultsols) soils; campo limpo is associated with lithosols (Lithic dystropepts) in the upper parts of the valley and with hydromorphic soils (Inceptsols) in the lower parts of the valley. In this study, differences in total root biomass and their variable structure and distribution among communities are likely the response to differences in chemical, physical, and moisture conditions of the soil that these four communities may have, in addition to genetic differences among plant species. The different community structure in the Cerrado gradient tends to reflect the differences in total root biomass. As aboveground biomass increased, root biomass also increased, and structural characteristics of the roots changed. The high amounts of total root biomass found in each community type may be an adaptation to frequent fires and annual drought, as I hypothesized. However, to confirm that hypothesis, comparisonsbetween similar community types, with the same environment conditions must be made by treating one with frequent burning while the other remains unburned.

Root biomass in Cerrado s.l. was not described before this study. When compared with other tropical savannas, the range of 16,317 kg ha^{-1} to 52,908 kg ha^{-1} for the Cerrado s.l. found in this study was quite high. Along a vegetation gradient from grassland to woodland in the Venezuelan llanos (a hyperseasonal savanna type which has a period of water shortage during the dry season and a period of excess of water during rain season), root biomass ranged from 11,480 to 18,910 kg ha^{-1} (Sarmiento and Vera 1979). In Lamto savanna, Ivory Coast, Africa, total root biomass ranged from 10,100 kg ha^{-1} to 19,000 kg ha^{-1} in the same gradient (Menaut and Cesar 1979).

Although total root biomass in the Cerrado s.l. was higher, root distribution by depth was similar to these other tropical savannas. Their root biomass also was concentrated in the surface soil layer for grasslands and more evenly dispersed though the soil for woodlands (Sarmiento and Vera 1979, Menaut and Cesar 1979). In campo limpo a decrease in root biomass in the deeper layers reflects the distinct root system that graminoids, the principal components in this community, display. Graminoid root systems are typified by shallow and widely spread roots along the top of the layer of soil. In campo sujo, cerrado aberto, and cerrado denso root biomass declined in a more gradual manner with increasing soil depth (Figure 3.1.). This is likely related to the increasing dominance of herbs, shrubs and trees (Table 3.2.) (Chapter 2). In cerrado denso, the greater abundance of roots in the 30 to 100 cm depth suggests a greater exploration of deeper soils. Lawson et al. (1968) reported a similar stratification of roots in Guinea savanna with large diameter roots of shrub and trees at depths of 20-30 cm which were overlain with a zone of grass roots in surface layers. Some species in Cerrado s.l. have been described as shallow-rooted such as *Echinolaena inflexa* (Poir) Chase, *Tristachya leiostachia* Nees (Poaceae), and some perennial herbs *Ipomoea villosa* Meissn. (Convolvulaceae), and *Vernonia grandiflora* Less (Compositae). Species with medium-rooted systems are represented by *Butia leiospatha* (Barb. Rodri.) Becc (Palmae), and *Jacaranda decurrens* Cham. (Bignoniaceae). Others, particularly evergreen trees such as *Dimorphandra mollis* Benth (Leguminosae), *Palicourea rigida* H.B.K. (Rubiaceae), *Qualea grandiflora* Mart. (Vochisiaceae) and *Kielmeyera coriacea* Mart. (Gutifereae) have been described as deep-rooted (Rawitscher 1948). The great diversity of species in Cerrado may be the a result of the interspecific coexistence of species, which allows for maximum explotation of water and nutrients at different depths because of variable root architecture.

The greatest proportion of the root biomass was concentrated in the top 30 cm of the soil horizon (more than 80%, except for cerrado denso). This was similar to Lamto Savanna in Africa where 80 % of the root biomass also occurs in surface soils (Menaut and Cesar 1979). However, roots have been reported to penetrate as deep as 19 m in the Brazilian Cerrado (Rawitscher 1948). A concentration of roots in the soil surface may also be related to the decomposition of organic matter, and the exploitation of nutrients in an ecosystem that is nutrient poor. Tropical savanna vegetation has a low rate of decomposition and nutrient availability during the dry season, but a much higher rate during the wet season (Swift et al. 1979). For cerrado s.s. and cerradão areas, litter decomposition is also higher during the wet season (Peres et al. 1983). Surface roots can rapidly capture nutrients available from decomposing organic matter, resulting in a very closed nutrient cycle in a nutrient-limited ecosystem (Jordan 1985). Leaching of nutrients during the wet season is thereby minimized. Surface roots also are well adapted to exploit the increased nutrient availability following frequent low intensity surface fires. Fire accelerates the process of mineralization of nutrients and increases the availability of nutrients through this mineralization and though ash deposition (McNabb and Cromack Jr 1990). Subsequently, a well developed root system in the upper limits of the soil surface facilitates survival after fire while allowing for rapid exploitation of available nutrients and limiting losses via leaching.

An important component of Cerrado s.l., fine roots (≤ 0.5 cm) are often related to the abundance of monocotyledons in grassland communities, and associated with herbs, shrubs and trees in the woodland (personal observation). Monocotyledons typically have a fibrous root system with a large number of adventitious roots which have very small diameters (Richards 1986). Monocotyledons form a continuous yet declining layer of biomass along the vegetation gradient from campo limpo to cerrado denso. The aerial biomass of graminoids along this gradient was 3,955 kg ha^{-1} (72 % of aboveground biomass) in campo limpo, 4,185 kg ha^{-1} (46 %) in campo sujo, 1,997 kg ha^{-1} (11 %) in cerrado aberto, and 1,670 kg ha^{-1} (13 %) in cerrado denso (Table 3.2.) (Chapter 2). Fine roots followed a similar decline in their relative contribution to the total root biomass as grasses did to aboveground biomass: 9,171 kg ha^{-1} (56 %) in campo limpo, 13,808 (46 %) in campo sujo, 18,630 kg ha^{-1} (40 %) for cerrado aberto, and 15,336 kg ha^{-1} (29%) for cerrado denso. In cerrado aberto and cerrado denso the increasing predominance of trees and shrubs with tap root systems, and of tubers promoted a greater diversity in the root diameter classes of these communities.

Tubers and other belowground structure occurred in all communities. They are adaptations to insure survival during the dry season through water and nutrient storage (Rizzini and Heringer 1961). Moreover, these belowground organs often possess dormant meristematic tissues (xilopodium) promoting vegetative reproduction. These are important adaptations in this environment with frequent fire. When aboveground tissues are destroyed by fire, shoots arise from xilopodia even in the absence of rain (Rizzini and Heringer 1961). Other species in the Cerrado s.l. have roots that run parallel to the ground (sucker roots) that produce shoots at variable intervals (Rizzini and Heringer 1962). In this study, some roots of 2.0-3.0 cm in diameter fit these description in cerrado aberto and cerrado denso.

Vegetative regeneration from belowground tissues is far more common that sexual reproduction in most grasses, trees and shrubs (Rizzini 1976). Seeds of different species subjected to a high temperature showed no increase in germination (Rizzini 1976). Seeds from species of herbaceous layer may be released from fruits after fire (Coutinho 1977). However, any established seedlings are subjected to drought, frequent fires and competition (Rizzini and Heringer 1962). Graminoids also have protected belowground buds that insure survival in spite of frequent fires (Rachid-Edwards 1956).

Cerrado s.l. had a high root:shoot ratio compared to tropical ecosystems (Table 3.3.). The high R:S ratio is thought to be an adaptation for drought and poor soil nutrient conditions (Monk 1966). Tropical dry forest, for example exhibit these conditions (Castellanos et al. 1991, Brown and Lugo 1992), however, the R:S ratio in Cerrado s.l. was three times higher.

In the Cerrado s.l., evergreen plants persist in an environment with a pronounced three to five month dry season; therefore, greater quantities of energy are allocated to roots to maximize exploitation of soil volume and hence the ability for water and nutrient absorption (Jesko 1992). Moreover, I think that frequent fire, which stimulates vegetative reproduction in Cerrado s.l., may be important agent in promoting a well-developed root biomass. A higher root:shoot (R:S) ratio was found in campo limpo and campo sujo (5.6 and 7.7 respectively), in contrast to that of cerrado aberto and cerrado denso (2.6 and 2.9). Root:shoot ratio of large individual species are expected to be lower than that of small species (Bray1963 in Monk 1966). The decrease in the R:S ratio in Cerrado s.l. occurred as woody vegetation increased.

Table 3.3. Root and aboveground biomass (Mg ha $^{-1}$) of different tropical ecosystem compared with Cerrado *sensu lato*.

ecosystem	tree density	shoot	root	r:s	source
Tropical Savanna					
Cerrado (Brazil)					
campo limpo	-	2.9	16.3	5.6	this study (1)
campo sujo	12	3.9	30.1	7.7	this study
cerrado aberto	1064	17.6	46.6	2.6	this study
cerrado denso	1000	18.4	53.0	2.9	this study
Llano (Venezuela)					
grassland	-	6.0	11.5	1.9	Sarmiento and Vera 1979 (2)
woody savanna	100	5.3	19.0	3.6	Sarmiento and Vera 1979
Ivory Coast (Africa)					
grassland	-	4.6	10.5	2.3	Menaut and Cesar 1979 (3)
woody savanna	250	5.4	13.8	2.6	Menaut and Cesar 1979
Tropical rain forest					
Brazil	10406	264.0	35.4	0.13	Nepstad 1989 (4)
Venezuela	nd	335.0	56.0	0.17	Jordan and Uhl 1978 and Stark and Spratt 1977 (5)
Ghana	5300	233.0	54.0	0.23	Greeland and Kowal 1960 (6)
Tropical dry forest					
Puerto Rico	12000	53.2	45.0	0.84	Murphy and Lugo 1986 (7)
Mexico	4700	73.6	31.0	0.42	Castellano et al. 1991 (8)

(1)- Aboveground biomass includes green grass, herbs, dicots, palms, bromeliads, shrubs and trees. Roots were measured up to 2.00 m in depth.

(2)- Root biomass was investigated up to 2.00 m in depth.

(3)- Aboveground and root biomass refer to the herb layer in these communities. Roots were investigated up to 2.00 m in depth.

(4)- Aboveground biomass includes live trees ≥ 1.0 cm in diameter, and root biomass was measured up to 10.0 m in depth.

(5) and (6)- Root biomass was measured up to 0.50 m and 0.90 m in depth, respectively..

(7)- Aboveground biomass includes all live vegetation > 1.50 m in height, standing dead material and epiphytes.

(8)- Aboveground biomass included trees, shrubs and lianas. Roots were measured to 0.80 m in depth.

Conclusion

This study investigated for the first time the belowground phytomass for plant communities along a vegetation gradient in the Brazilian cerrado. The increase in root biomass from campo limpo to cerrado denso was similar to earlier findings concerning aboveground biomass in the same study area. Although roots were measured to a depth of 2.00 m, they were concentrated in the upper limits of the soil with $\geq$ 71 % in the top 30 cm.

Remarkable quantities of phytomass of the Cerrado s.l. were belowground. Reasons for this may be the presence of nutrient-poor soils and periods of drought, high vegetative reproduction stimulated by fire, and better exploitation of nutrients and water by volume of soil. Roots are a reservoir of nutrients, C and water. The allocation and storage of C was different from that of tropical rain forests which have similarly nutrient-poor soils. Consequently, the Brazilian Cerrado gradient may be a more significant global C pool than previously thought. While fires may not result in significant C losses of the Cerrado vegetation, if it is deforested, burned and replaced by crop monoculture, belowground C pools may be depleted. Moreover altering the carbon budget through belowground C depletion, large-scale crop conversions will probably result in great losses of plant diversity in this ecosystem.

Reference

Askew, G. P., D. J. Moffatt, R. F. Montgomery, and P. L. Searl. 1971. Soils and soil moisture as factors influencing the distribution of the vegetation formations of the Serra do Roncador, Mato Grosso. Pages 150-170 .In: M. G. Ferri, editor. III Simposio sobre o cerrado. Editora Edgard Blucher Ltda & Editora da Universidade de São Paulo, São Paulo.

Böhn, W. 1979. Methods of studying root systems. Springer-Verlag, New York.

Brown, S., and A. E. Lugo. 1993. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8-18.

Castellanos, J., M. Maass, and J. Kummerow. 1991. Root biomass of a dry decidous tropical forest in Mexico. Plant and Soil . (131):225-228.

Coutinho,L. M. 1977. Aspectos ecológicos do fogo no cerrado. II As queimadas e a dipersão de sementes em algumas especies anemocóricas do estrato herbaceo subarbustivo. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Botânica 5:57-64

Coutinho, L. M. 1978b. O conceito de cerrado. Revista Brasileira de Botânica 1:17-23.

Eiten, G. 1972. The cerrado vegetation of Brazil. Botanical Review (38):201-341.

Fearnside, P. M. 1992. Greenhouse gas emissions from deforastation in the Brazilian Amazon. in: W. Makundi and J. Sathaye, editors. Carbon emissions and sequestration in forests: case studies from seven developing countries, Draft Edition. Volume 2. U.S. Environmental protection Agency, Climate Change Division, Washington, DC and Energy and Environment Division,Lawrence Berkeley Laboratory, Berkeley, CA, .

Goodland, R., and R. Pollard. 1973. The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology (61):219-224.

Greeland, D. J., and J. M. L. Kowal. 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12(2):154-173.

Haridasan, M. 1990. Solos do Distrito Federal. Pages 309-330 in M. N. Pinto, editor. Cerrado: Caracterização, Ocupação e Perspectivas. Editora da UnB, Brasilia.

Harris, W. F., P. Sollins, N. T. Edwards, B. E. Dinger, and H. H. Sugharet. 1972. Analysis of carbon flow and productivity in a temperate deciduous forest ecosystem. Pages 116-122 in: D. E. Reichle, J. F. Franklin and D. W. Goodwall, editors. Productivity of World Ecossytem. National Academyof Science, Washington, DC.

Jesko, T. 1992. The root as an integral part of the plant. Pages 1-29 .Iin: J. Kolek and V. Kozinka, editors. Physiology of the Plant Root System. Volume Development in Plant and Soil Sciences, 46. Kluwer Academic Plublishers, Czechoslovakia.

Jordan, C. F. 1985. Nutrient Cycling in Tropical Forest Ecosystem. Wiley, Chichester. 190 p.

Jordan, C. F., and C. Uhl. 1978. Biomass of a "tierra firme' forest of the Amazon Basin. Oecologia Plantarum 13:387-400.

Kerfoot, O. 1963. Ther root systems of tropical forest trees. Commonwealth Forestry Review (42):19-26.

Lawson, G. W., J. Jenik, and K. O. Armstrong-Mensah. 1968. A study of a vegetation catena in Guinea savanna ar Mole Game Reserve (Ghana). Journal of Ecology (56):505-522.

McNabb, D. H., and K. Cromack Jr. 1990. Effects of prescribed fire on nutrients and soil productivity. Pages 125-142 in: J. D. Walstad, S. R. Radosevich and D. V. Sandberg, editors. Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State Press, Corvallis, OR.

Menaut, J. C., and J. Cesar. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. Ecology:1197-1210.

Monk, C. 1966. Ecological importance of root/shoot ratios. Bulletin of the Torrey Botanical Club 93(6):402-406.

Murphy, P. G. and A. E. Lugo 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18(2):89-96.

Nepstad, D. C. 1989. Forest regrowth in abandoned pastures of eastern Amazonia; limitations to tree seedling survival and growth. Ph.D. Dissertation. Yale University.

Peres, J. R., A. R. Suhet, M. A. T. Vargas, and A. Drozdowicz. 1983. Litter production in areas of Brazilian "Cerrados". Boletim de Pesquisa Agropecuaria Brasileira 18(9): 1037-1043.

Rachid-Edwards, M. 1956. Alguns dispositivos para proteção de plantas contra a seca e o fogo. Boletim da Faculdade de Filosofia, Ciências e Letras da USP (13):37-69.

Rawitscher, F. 1948. The water economy of the vegetation of the campos cerrados in southern Brazil. Journal of Ecology 36(2):237-268.

Richards, J. H. 1986. Root form and depth distribution in several biomes. in: C. Carlisle, W. L. Berry, I. R. Kaplan and Watterson, editors. Mineral exploration: Biological Systems and Organic Matter. Volume V. Prentice Hall, Englewood cliffs, New Jersey.

Rizzini,C.T. 1976. Tratado de Fitogeografia do Brasil. Editora Hucitec e Editora da USP, São Paulo. 327 p.

Rizzini, C. T., and E. P. Heringer. 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phyton 17(1):105-124.

Rizzini, C. T., and E. P. Heringer. 1962. Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. Anais da Academia Brasileira de Ciências (34):235-247.

Russel, R. S. 1977. Plant root systems; their function and interaction with the soil. McGraw-Hill, London.

Sanford Jr, R. L. 1989. Root systms of three adjacent, old growth Amazon forests and associated transition zones. Journal of Tropical Forest Science 1(3):268-279.

Santantonio, D., R. K. Hermann, and W. S. Overton. 1977. Root biomass studies in forest ecosystem. Pedobiologia (17):1-31.

Sarmiento, G., and M. Vera. 1979. Composicion, estructure, biomassa y produccion de differentes sabanas en los Llanos de Venezuela. Boletin de la Sociedade Venezolana de Ciencias Naturales (136):5-41.

Sokal, R. R., and F. J. Rohlf, editors. 1981. Biometry - The Principles and Practice of Statistics in Biological Research, 2nd Edition. W.H. Freeman and Company, New York.

Stark, N., and M. Spratt. 1977. Root biomass and nutrient storage in Rainforest Oxisols near San Carlos de Rio Negro. Tropical Ecology(18):1-9.

Swift, M. J., O. W. Heal, and J. M. Anderson, editors. 1979. Decomposition in Terristerial Ecosystem. Volume Studies in Ecology, 5. Blackwell, London.

CHAPTER 4
CARBON, NITROGEN, AND SULFUR POOLS, AND DYNAMICS ALONG A VEGETATION GRADIENT IN THE BRAZILIAN CERRADO

Abstract

Nutrient pools and fire effects on nutrients were investigated in four plant communities of Cerrado *sensu lato* gradient in central Brazil. This gradient consists of campo limpo (pure grassland), campo sujo (grassland with sparse shrubs), cerrado aberto and cerrado denso (both are variants of cerrado *sensu stricto,* which comprises grasses, herbs, shrubs and trees).

Aboveground pools of carbon (C), nitrogen (N) and sulfur (S) varied from 1,933, 15, and 1.7 kg ha^{-1}, respectively, in campo limpo to 12,809, 185, and 15.3 kg ha^{-1}, respectively, in cerrado denso. Root pools were measured to a depth of 2.00 m. Roots $\leq$ 0.5 cm in diameter had the largest pool for all nutrients. Tubers, a subterranean organ of reserve, tended to have the highest concentration of nutrients. Total root nutrient pools were generally at least two times larger than aboveground pools. Cerrado *sensu lato* root C pools ranged from 7,633 to 25,482 kg ha^{-1}; N pools varied from 127 to 369 kg ha^{-1}; and S pools were 8 to 21 kg ha^{-1} for campo limpo and cerrado denso, respectively. Soil nutrient pools accounted for more than 86 % of the total ecosystem nutrients. Campo limpo had the highest C and N soil pools, but S was highest in the cerrado aberto soil pool.

Fire reduced all aboveground pools. Except for N in cerrado aberto, nutrient losses were greater by volatilization than by ash particulate. Losses of nutrients in all ecosystem pools as the result of fire were < 2.0 %.

Compared with other tropical ecosystems, the belowground storage of nutrients in Cerrado was unique that can be a large sink or source of C and other nutrients. Fire in

Cerrado *sensu lato* released 1/10 or less of the nutrients lost from tropical moist and dry forests through slash-and-burning agriculture methods. However, deforestation of Cerrado *sensu lato* may make available to the atmosphere masses of C and nutrients that are currently sequestered in root and soil pools.

Introduction

The Brazilian Cerrado (Cerrado *sensu lato*) is a gradient of plant communities of diverse compositions and structures. This vegetation gradient is comprised of campo limpo (grassland), campo sujo (grassland with sparse shrubs), campo cerrado (open shrub), cerrado *sensu stricto* (a dense scrub made up of shrubs and trees), and cerradão (a forest with a more or less closed tree canopy) (Goodland 1971, Eiten 1972, Coutinho,1978b).

Cerrado s.l. is located in central Brazil and has an areal extent of approximately 2.0 million km^2. Its tropical climate is characterized by distinct wet and dry seasons. Precipitation ranges from 700 to 2000 mm, concentrated between October and March. Temperature varies little during the year, ranging from 20 °C to 26 °C (Eiten 1972). The majority of soils are deep and well drained Latosols, recognized as Oxisols in the American Soil Taxonomy. These soils are nutrient poor, with a high concentration of aluminum and low cation exchange capacity (Alvim and Araujo 1952, Lopes and Cox 1977). In addition to climatic and soil factors, fire has been also considered to be a strong influence on plant structure, composition, and productivity in Cerrado s.l. (Coutinho 1990). Fires have been suggested as a significant influence in the evolutionary history of Cerrado (Lofgren 1898; Warming 1973). Charcoal evidence suggests the presence of fire in the region for at least 8600 years (Coutinho 1981). Burning occurs accidently, intentionally by human ignition, or rarely by lighting. Fire accelerates nutrient cycling through conversion of organic materials into mineral forms available to plants (Coutinho 1990). Fires also result in nutrient losses to the atmosphere via particulate and volatilization (Kauffman et al. 1994). Carbon (C), nitrogen (N), and sulfur (S) are essential elements present in plant tissues and organic debris, which are easily affected by fire because of their low temperatures of volatilization (Raison et al. 1985, Kauffman et al.1992). Emissions of C, N, and S from biomass burning of world tropical savannas have been reported to have a strong influence on global atmospheric chemistry (Crutzen and Andreae 1990).

Adaptation to a short fire return interval (two to three years) in Cerrado s.l. includes the ability of plants to persist and/or rapidly recover following fire (Eiten 1972, Pivello and Coutinho 1992). Fire effects on vegetation have been described at community, population, and species levels (Coutinho 1977, Cesar 1980, Raw and Hay 1985, Ramos 1990, Rosa 1990). Nutrient content in the biomass was reported for campo sujo by Batmanian (1983), and for campo limpo, campo sujo, campo cerrado, and cerrado *sensu stricto* by Kauffman et al. (1994). Cavalcanti (1978) recorded soil nutrient concentration of campo cerrado after burning. Concentration of Ca, K, P, and Mg in the top 5 cm in the soil increases after fire and decreases in the following months. Mineral nutrient inputs occur during the rainy season, but fires near a study area may introduce nutrients by dry fall (Coutinho 1979). Season of burning in campo cerrado did not affect in the amount of nutrient losses to atmosphere due to fire (Pivello and Coutinho 1992). Fuel load, fire behavior, and fire effects on nutrient dynamics were described by Kauffman et al. (1994). However, total aboveground nutrient pool, root nutrient pool and total ecosystem nutrient pools of Cerrado s.l. have not been described.

Natural vegetation of Cerrado s.l. has been changing at accelerating rates. Thirty-seven percent of Cerrado s.l. is already modified by cities, dams, mining, abandoned agriculture, and also by the cultivation of pastures, soybeans, corn , rice, coffee and eucalyptus (Dias 1990). Given this level of land-use conversion and the extent of burning, data on nutrient pools are important in order to understand the significance of the Cerrado ecosystem both as source and sink for carbon and other nutrients.

In order to understand the consequences of fire and land use on the nutrient dynamics, the following objectives were established: (1) to quantify C, N, and S nutrient pools in the aboveground biomass for four plant communities of the vegetation gradient of cerrado *sensu lato*; (2) to quantify belowground (soil and roots) C, N, and S pools for each community type; and (3) to quantify losses of nutrients to the atmosphere during fires, and amounts remaining following fire for each community type.

Study Site

The research was conducted at the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatistica (IBGE Ecological Reserve) and at the Estação Ecológica do Jardim Botânico de Brasilia (JBB Ecological Reserve). They are located approximately 35 km south of Brasilia, DF, Brazil (15^{o} 51' S and 47^{o} 63' W). The elevation is 1,100 m and slopes are < 10%. During the period from 1980 to 1992, mean annual temperature varied from 19.2 ^{o}C to 22.4 ^{o}C. Mean precipitation was 1482 mm distributed in two distinctive seasons, the wet season from October to March with 1257 mm and the dry season from April to September with 225 mm. Mean maximum relative humidity was 81% in December, and the mean minimum was 55% in August (File data from Estação Agroclimatológica do IBGE 1980-1992).

Vegetation in these Ecological Reserves is distributed in mosaics of community types described earlier, plus intermediate forms that were shaped by fire. In this study, four community types were investigated: campo limpo and campo sujo (already described) and cerrado aberto and cerrado denso, both variants of cerrado *sensu stricto*. Cerrado aberto had a more open and less dense tree canopy compared to cerrado denso.

Methods

Aboveground vegetation and nutrient pools

Aboveground nutrient pools were divided into litter, woody debris, graminoids (dry and green), herbs (small dicots), shrubs (leaves and total), and trees. These were the main components partitioned to describe aboveground biomass of these communities (Chapter 2). Mass of C, N, and S was calculated utilizing plant nutrient concentrations from the same study area reported by Kauffman et al. (1994) (Appendix 4.1). To calculate nutrient pools, nutrient concentration in each component was multiplied by its respective biomass reported in Chapter 2. Some minor components in this study (e.g. litter and dicots in campo limpo, and shrubs and trees in campo sujo) were not included in the estimation of nutrient mass because nutrient concentration for these components were not provided by Kauffman et al. (1994). Nutrient mass of cerrado aberto and cerrado denso, were calculated according to the nutrient concentration of campo cerrado and cerrado *sensu stricto* of Kauffman et al. (1994). Nutrient concentration of wood debris for cerrado aberto and denso was that of cerrado *sensu stricto*. To determine nutrient mass concentration of trees, I used the concentration means from unpublished data (Dr. Kauffman in a pers. com.) (Appendix 4.2). After fire, the nutrient concentration and pools of residual biomass were calculated utilizing the same nutrient concentration applied for calculating nutrient mass before fire. I assumed that nutrient concentration in residual biomass did not change significantly due to fire. Ash nutrient concentration for each fire was determined because the variability of individual fires influences the concentration and mass of nutrients in ash. Ash samples for nutrient analyses were the same as for ash mass determination (Chapter 2); five samples were collected for each community type. Carbon, N and S concentration in ash were analyzed using the induction furnace technique with Carlo Erba NA Series 1500.

Belowground nutrient pools

Belowground nutrient pools included root and soils to a depth of 2.00 m. Roots were classified on the basis of their diameter; size classes were ≤0.5 cm, 0.6-1.0 cm, 1.1-2.0 cm, 2.1-3.0 cm, and tubers. These were the same diameter classes used for root biomass quantification (Chapter 3). Nutrient concentration of five samples, randomly chosen, for each diameter class was determined for each community type. Nutrient mass in roots was calculated through multiplication of biomass in that diameter class by the mean nutrient concentration for each root diameter class. Soil nutrient concentration (N=5) was measured in each community type for the same depth intervals as root biomass quantification (i.e. 0-10 cm, 10-20 cm, 20-30 cm, 30-50 cm, 50-100, and 100-200 cm) (Chapter 3). Root samples were dried at 60 °C for 48 hours, and soil samples were air dried. Both were analyzed for C, N, and S concentration using a induction furnace method with Carlo Erba NA Series 1500. Soil mass was calculated from bulk density determined for the same depth intervals. After a monolith block was taken for root biomass studies, a bulk density sampler with a known ring volume was used to take samples from the wall of the soil pit. For sampling root biomass at 100 - 200 cm depth, an auger was used to a depth of 1.50 m. In the bottom of the hole, I collected a bulk density sample using the same sampler. Five samples were collected for each depth interval for each community type. Samples were dried at 60 °C for 48 hours, weighed, and their bulk density calculated. (Appendix 4.3.).

Differences in nutrient concentration and nutrient pools among communities for aboveground and belowground pools were tested using Analysis of Variance (ANOVA). If assumptions of normality and equal variance were not assumed, log transformation were applied to the data. However, since data with log transformation had the same result as data without log transformation, results are presented without log transformation. If at least one community had concentrations or nutrient masses differing from other communities, the least significant test was applied to detect differences (p-value = 0.10) (Sokal and Rohlf 1981).

Results

Aboveground pools

Total aboveground biomass in Cerrado s.l. was 5,542 kg ha^{-1} for campo limpo, 7,523 kg $ha^{-1}$for campo sujo (excluding litter, dicot and tree components), 24,847 kg ha^{-1} for cerrado aberto, and 24,944 kg ha^{-1} for cerrado denso (Chapter 2, Table 2.1.).

Similar to aboveground biomass, nutrient pools of C, N, and S increased along the gradient from campo limpo to cerrado denso (Table 4.1.). Carbon pools ranged from 1,833 to 12,809 kg ha^{-1}, N pools from 15 to 185 kg ha^{-1}, and S pools from 1.7 to 15.2 kg ha^{-1} (Table 4.1.). There were no significant differences in the total nutrient pools between cerrado aberto and cerrado denso for any nutrient (Table 4.1.). Aboveground S pools in campo limpo and campo sujo were significantly different. However, no differences were detected between campo limpo and campo sujo for C and N (Table 4.1.). Woodland communities (cerrado aberto and cerrado denso) had at least 3-fold

Table 4. 1. Total nutrient pools (kg ha^{-1}) in Cerrado *sensu lato*, near Brasilia,DF, Brazil. Numbers are means ± standard error. Numbers in parenthesis are the relative proportion (%) of each component within aboveground, roots and soil pools.

	CARBON											
	campo limpo			campo sujo			cerrado aberto			cerrado denso		
ABOVE												
wd* < 0.64	-			-			161 ± 25		(1)	148 ± 14		(1)
wd > 0.64	-			-			796 ± 78		(7)	816 ± 104		(6)
litter	-			960 ± 157	a	(27)	2,572 ± 193	b	(21)	1,791 ± 138	c	(14)
dry graminoids	957 ± 66	a	(51)	1,602 ± 148	b	(44)	1,059 ± 103	a	(9)	676 ± 60	c	(5)
green graminoids	926 ± 67	ab	(49)	374 ± 45	b	(10)	177 ± 15	c	(1)	147 ± 12	c	(1)
dicot	-			701 ± 110		(19)	793 ± 88		(7)	855 ± 92		(7)
leaf-shrub	-			-			384 ± 39			216 ± 25		
total -shrub	-			-			3,216 ± 289	a	(26)	1,513 ± 197	b	(12)
trees	-			-			3,386 ± 956		(28)	6,863 ± 1345		(54)
total	1,833 ± 112	a		3,637 ± 413	a		12,160 ± 788	b		12,809 ± 1511	b	
ROOT(diameter class)												
< 0.6 cm	4,270 ± 445	a	(56)	6,885 ± 434	b	(16)	9,092 ± 725	c	(40)	7,487 ± 1116	bc	(29)
0.6-1.0	439 ± 183	a	(6)	2,478 ± 568	b	(16)	3,795 ± 573	c	(17)	2,698 ± 486	bc	(11)
1.1-2.0	1,513 ± 947	a	(20)	2,866 ± 761	a	(19)	3,262 ± 728	a	(14)	5,475 ± 960		(22)
2.1-3.0				1,702 ± 867		(11)	1,506 ± 703		(6)	4.610 ± 1295		(18)
tuber	1,411 ± 672		(18)	1,158 ± 760		(8)	5,335 ± 1993		(23)	5,213 ± 2908		(20)
total	7,633 ± 1177	a		15,088 ± 2250	b		22,990 ± 3009	c		25,482 ± 4091	c	
SOIL(depth class)												
0-10	42,972 ± 1805	a	(17)	27,867 ± 2956	b	(13)	31,286 ± 1914.5	b	(12)	31,991 ± 869	b	(12)
10-20	36,493 ± 2602	a	(15)	20,980 ± 1580	b	(10)	25,620 ± 773.2	c	(10)	24,967 ± 622	b	(10)
20-30	26,615 ± 2785	a	(11)	20,080 ± 988	b	(10)	22,473 ± 965.9	b	(9)	23,052 ± 579	ab	(9)
30-50	27,347 ± 4828		(11)	21,757 ± 1060		(10)	25,352 ± 409.0		(10)	25,207 ± 667		(10)
50-100	44,726 ± 1829	a	(18)	45,140 ± 2531		(21)	53,356 ± 2164.4	b	(21)	55,415 ± 2861	b	(22)
100-200	67,833 ± 2278	a	(28)	74,951 ± 5378	a	(36)	98,905 ± 2728.0	b	(38)	94,418 ± 3236	b	(37)
total	245,986 ± 6069	a		210,774 ± 12436	b		256,992 ± 7331.1	a		255,050 ± 6775	a	
TOTAL SYSTEM	255,453			229,500			292,142			293,342		

*wd means wood debris. Different letters denote a significant difference ($P \leq 0.10$) when testing carbon mass among the communities of Cerrado *sensu lato*, near Brasilia, DF, Brazil. The absence of letters denotes no statistical differences among communities. Dashes (-) denote that components were not found in the community.

Table 4.1. Continued

	NITROGEN											
	campo limpo			campo sujo			cerrado aberto			cerrado denso		
ABOVE												
wd* < 0.64	-			-			1.6 ± 0.2		(1)	1.5 ± 0.1		(1)
wd > 0.64	-			-			5.3 ± 0.5		(3)	5.7 ± 0.7		(3)
litter	-			13.4 ± 2.2	a	(34)	35.7 ± 2.7	b	(22)	25.8 ± 2.0	c	(14)
dry graminoids	5.3 ± 0.4	ab	(35)	9.6 ± 0.9	c	(25)	6.9 ± 0.7	a	(4)	4.6 ± 0.4	b	(6)
green graminoids	9.8 ± 0.7	a	(65)	4.5 ± 0.5	b	(12)	2.4 ± 0.2	c	(2)	1.7 ± 0.1	c	(1)
dicot	-			11.3 ± 1.8		(29)	12.1 ± 1.3		(7)	11.7 ± 1.3		(6)
leaf-shrub	-			-			9.2 ± 0.9	a		4.4 ± 0.5	b	
total -shrub	-			-			44.5 ± 4.0	a	(27)	19.1 ± 2.5	b	(10)
trees	-			-			56.8 ± 16.0	a	(34)	115.2 ± 22.6	b	(62)
total	15.1 ± 0.9	a		38.9 ± 5.7	a		165.3 ± 12.4	b		185.3 ± 24.4	b	
ROOT(diameter class)												
< 0.6 cm	72.7 ± 28.1	a	(57)	82.3 ± 3.8	ab	(46)	128.5 ± 11.3	b	(40)	106.6 ± 13.8	b	(29)
0.6-1.0	10.6 ± 4.2	a	(8)	29.7 ± 5.2	b	(17)	55.3 ± 10.9	c	(17)	40.6 ± 8.1	bc	(11)
1.1-2.0	31.6 ± 26.6		(25)	32.9 ± 9.0		(19)	40.1 ± 10.7		(13)	82.8 ± 9.3		(22)
2.1-3.0	-			18.9 ± 11.2		(11)	21.9 ± 14.2		(7)	62.3 ± 21.9		(17)
tuber	12.4 ± 4.5		(10)	12.5 ± 6.3		(7)	74.7 ± 31.6		(23)	76.6 ± 31.5		(21)
total	127.4 ± 33.9	a		176.3 ± 23.1	a		320.5 ± 40.9	b		368.8 ± 51.2	b	
SOIL(depth class)												
0-10	2,676 ± 110.7	a	(15)	1,964 ± 262.9	b	(16)	1,903 ± 72.4	b	(12)	2,100 ± 62.1	b	(12)
10-20	2,401 ± 126.5	a	(14)	1,467 ± 121.7	b	(12)	1,712 ± 97.1	b	(10)	1,725 ± 71.4	b	(10)
20-30	1,911 ± 156.0	a	(11)	1,355 ± 110.7	b	(11)	1,528 ± 95.7	b	(9)	1,527 ± 98.2	b	(9)
30-50	2,120 ± 266.0	a	(12)	1,303 ± 45.6	b	(11)	1,586 ± 196.9	b	(10)	1,556 ± 103.3	b	(10)
50-100	3,590 ± 160.7	a	(20)	2,203 ± 100.3	b	(18)	3,229 ± 321.8	a	(21)	3,219 ± 365.0	a	(22)
100-200	5,022 ± 179.5		(28)	3,859 ± 405.3		(32)	4,735 ± 385.3		(38)	4,964 ± 373.9		(37)
total	17,720 ± 395.6	a		12,150 ± 863.4	b		14,694 ± 470.5	c		15,091 ± 904.7	c	
TOTAL SYSTEM	17,862			12,365			15,180			15,645		

*wd means wood debris. Different letters denote a significant difference ($P \leq 0.10$) when testing nitorgen mass among the communities of Cerrado *sensu lato*, near Brasilia, DF, Brazil. The absence of letters denotes no satatiscal differences among communities. Dashes (-) denote that components were not found in the community.

Table 4.1. Continued

	SULFUR											
	campo limpo			campo sujo			cerrado aberto			cerrado denso		
ABOVE												
wd* < 0.64	-			-			0.1 ± 0.0		(1)	0.1 ± 0.0		(1)
wd > 0.64	-			-			0.5 ± 0.0		(3)	0.5 ± 0.1		(3)
litter	-			1.4 ± 0.2	a	(21)	4.1 ± 0.3	b	(27)	2.7 ± 0.2	c	(18)
dry graminoids	0.8 ± 0.1	a	(45)	1.2 ± 0.1	b	(17)	0.8 ± 0.1	a	(5)	0.5 ± 0.0	c	(4)
green graminoids	0.9 ± 0.1	a	(55)	0.5 ± 0.1	b	(8)	0.3 ± 0.0	c	(2)	0.2 ± 0.0	c	(1)
dicot	-			3.7 ± 0.6	a	(54)	1.3 ± 0.1	c	(9)	1.5 ± 0.2	b	(10)
leaf-shrub	-			-			1.0 ± 0.1	a		0.4 ± 0.1	b	
total -shrub	-			-			4.4 ± 0.4	a	(28)	1.8 ± 0.2	b	(12)
trees	-			-			3.8 ± 1.1	a	(25)	7.7 ± 1.5	b	(51)
total	1.7 ± 0.1	a		6.7 ± 0.9	b		15.3 ± 0.9			15.2 ± 1.7	c	
ROOT(diameter class)												
< 0.6 cm	4.8 ± 2.0		(59)	5.6 ± 0.4		(45)	7.1 ± 0.6		(42)	5.7 ± 0.4		(27)
0.6-1.0	0.5 ± 0.2	a	(6)	1.6 ± 0.3	b	(14)	2.7 ± 0.5	b	(16)	2.2 ± 0.5	b	(11)
1.1-2.0	1.9 ± 1.6		(24)	2.0 ± 0.5		(16)	1.8 ± 0.4		(11)	4.6 ± 0.4		(22)
2.1-3.0				2.1 ± 1.5		(17)	1.0 ± 0.5		(6)	3.4 ± 1.1		(16)
tuber	0.8 ± 0.3		(11)	1.0 ± 0.5		(8)	4.2 ± 1.5		(25)	5.1 ± 2.5		(24)
total	8.0 ± 2.5	a		12.2 ± 2.5	ab		16.7 ± 1.9	bc		21.0 ± 3.6	c	
SOIL(depth class)												
0-10	124.3 ± 5.9	a	(5)	138.4 ± 15.4	ab	(5)	308.0 ± 17.7	c	(8)	174.0 ± 24.3	b	(11)
10-20	134.0 ± 11.5	a	(5)	130.2 ± 26.7	a	(5)	202.3 ± 10.7	b	(5)	132.3 ± 15.1	a	(9)
20-30	131.1 ± 4.9	a	(5)	163.5 ± 17.2	a	(5)	198.1 ± 16.6	b	(5)	132.9 ± 10.8	a	(9)
30-50	183.3 ± 10.3	a	(7)	231.8 ± 29.7	a	(8)	322.6 ± 47.5	b	(9)	156.6 ± 16.3	a	(10)
50-100	755.7 ± 133.7	a	(29)	677.0 ± 12.7	a	(23)	761.1 ± 103.1	a	(21)	157.3 ± 11.6	b	(10)
100-200	1,301.1 ± 86.3	a	(49)	1,607.3 ± 211.5	ab	(54)	1,928.4 ± 265.6	b	(51)	776.5 ± 50.4	c	(51)
total	2,629.5 ± 175.1	a		2,948.3 ± 282.0	a		3,720.5 ± 403.1	b		1,529.6 ± 66.8	c	
	2,639.3			2,967.2			3,752.5			1,565.8		

*wd means wood debris. Different letters denote a significant difference ($P \leq 0.10$) when testing sulfur mass among the communities of Cerrado *sensu lato*, near Brasilia, DF, Brazil. The absence of letters denotes no statistical differences among communities. Dashes (-) denote that components were not found in the community.

more aboveground total C mass than grassland communities (campo limpo and campo sujo); N mass was 4-fold more and S mass was 2-fold more. Nutrient pools in campo limpo and campo sujo were predominantly in graminoids. In contrast, in cerrado aberto and cerrado denso communities had the occurrence of shrubs and trees, which accounted for between 54% and 72% of their total nutrient pools.

Fine roots (≤ 0.5 cm) contributed the majority of nutrient mass in all communities (Table 4.1.). However, while in campo limpo more than 55 % of C, N, and S mass was in this diameter class, in cerrado denso only 29 % was presented in the fine roots. In cerrado denso, root nutrient mass was more evenly distributed among other diameter classes. Tubers of cerrado aberto and cerrado denso had higher nutrient pools than did and cerrado denso communities had the occurrence of shrubs and trees, which accounted for between 54% and 72% of their total nutrient pools.

Root nutrient concentration and mass

Nutrient concentration tended to be higher in tubers than in roots of all diameter classes, except in the campo limpo community, although statistically differences were not detected. For example, tuber N concentration in cerrado denso was 1.25 % while roots ≤ 0.5 cm and 0.6-1.0 cm in diameter had 0.71 %; 1.1-2.0 cm had 0.77 %; and 2.1-3.0 cm had 0.62 %. Carbon concentration in the roots of campo limpo tended to be lower than in campo sujo, cerrado aberto, and cerrado denso. On the other hand, N and S concentrations in the roots of campo limpo tended to be higher than in the other communities (Table 4.2.).

Table 4.2. Nutrient concentrations (%) of roots by diameter, and tubers along a vegetation gradient in Cerrado *sensu lato*, near Brasilia, DF, Brazil.

CARBON

	campo limpo		campo sujo		cerrado aberto		cerrado denso	
<0.6	46.74 ± 1.18	a	49.92 ± 0.42	b	48.78 ± 0.05	b	48.7 ± 0.12	b
0.6-1.0	44.66 ± 1.27	a	50.19 ± 0.55	b	49.05 ± 0.43	bc	48.26 ± 0.16	c
1.1-2.0	48.70 ± 1.51	ac	50.89 ± 0.70	b	49.70 ± 0.11	bc	47.07 ± 0.22	a
2.1-3.0	-		51.82 ± 0.31	a	50.03 ± 0.58	b	47.97 ± 0.33	c
tuber	47.11 ± 1.03		48.48 ± 0.90		49.98 ± 1.03		47.62 ± 0.69	

NITROGEN

	campo limpo		campo sujo		cerrado aberto		cerrado denso	
<0.6	0.75 ± 0.24		0.60 ± 0.02		0.68 ± 0.02		0.71 ± 0.06	
0.6-1.0	1.13 ± 0.16	a	0.63 ± 0.06	b	0.69 ± 0.06	b	0.71 ± 0.75	b
1.1-2.0	0.71 ± 0.27		0.56 ± 0.03		0.57 ± 0.05		0.77 ± 0.13	
2.1-3.0	-		0.63 ± 0.34		0.63 ± 0.24		0.62 ± 0.10	
tuber	0.56 ± 0.11		0.68 ± 0.19		0.72 ± 0.14		1.25 ± 0.45	

SULFUR

	campo limpo	campo sujo	cerrado aberto	cerrado denso
<0.6	0.049 ± 0.017	0.040 ± 0.002	0.038 ± 0.001	0.039 ± 0.004
0.6-1.0	0.059 ± 0.013	0.036 ± 0.006	0.034 ± 0.003	0.039 ± 0.060
1.1-2.0	0.044 ± 0.015	0.035 ± 0.003	0.026 ± 0.017	0.042 ± 0.004
2.1-3.0	-	0.071 ± 0.051	0.032 ± 0.003	0.033 ± 0.005
tuber	0.04 ± 0.013	0.062 ± 0.028	0.042 ± 0.050	0.081 ± 0.032

Numbers are means followed by standard error. Different letters denote a significant difference (P-value < 0.10) in concentration when testing among communities using LSD test. No letters denotes no statistically differences among comunity types.

Root biomass in Cerrado *sensu lato* was 16,317 kg ha^{-1} in campo limpo, 30,083 kg ha^{-1}in campo sujo, 46,584 kg ha^{-1} in cerrado aberto, and 52,908 kg ha^{-1} in cerrado denso (Chapter 3, Table 3.1.). Carbon mass ranged from 7,633 kg ha^{-1} in campo limpo to 25,482 kg ha^{-1} in cerrado denso, the N pool ranged from 127 kg ha^{-1} in campo limpo to 369 kg ha^{-1} in cerrado denso, and the S pool was 8 kg ha^{-1} in campo limpo to 21 kg ha^{-1} in cerrado denso (Table 4.1.). Total C, N, and S pools in the roots of cerrado aberto were not significantly different from those of cerrado denso, while the total C pool in campo limpo was significantly different from that of campo sujo, but the N pools or S pools were not. Fine roots ($\leq$ 0.5 cm) contributed the majority of nutrient mass in all communities (Table 4.1.). However, while fine roots contained 55 % of C, N and S mass in campo limpo, in cerrado denso only 29 % was present in fine roots. In cerrado denso, root nutrient mass was more evenly distributed among other diameter classes. Tubers of cerrado aberto and cerrado denso had higher nutrient pools than did tubers from campo limpo and campo sujo. Carbon mass in tubers was at least 1.5-times greater in woodlands than in grasslands. Nitrogen mass in tubers was approximately in 1.8-times greater in woodland; and S mass in tubers was 1.4-times greater woodlands than in grasslands.

Soil nutrient concentration and mass

Soil nutrient concentration was distributed differently among depths (Table 4.3.). Carbon and N were highest at surface soils and decreased with depth up to 2.00 m. Campo limpo had the highest C and N concentration among the communities sampled, and there was a slight increase in concentration of C and N from campo sujo to cerrado denso (not statistically significant). Sulfur concentration in soils of campo limpo, campo sujo, and cerrado aberto did not vary among depths. For example S concentrations in

Table 4.3. Concentration (%) of carbon, nitrogen, and sulfur in soils to depth of 2 m along a vegetation gradient of Cerrado *sensu lato*, near Brasilia, DF, Brazil.

CARBON

soil depth(cm)	campo limpo	campo sujo	cerrado aberto	cerrado denso
0-10	4.63 ± 0.087 a	3.00 ± 0.318 b	3.37 ± 0.092 b	3.44 ± 0.042 b
10-20	3.64 ± 0.116 a	2.09 ± 0.158 b	2.55 ± 0.034 b	2.49 ± 0.028 b
20-30	2.37 ± 0.111	1.79 ± 0.088	2.01 ± 0.039	2.06 ± 0.023
30-50	1.61 ± 0.127	1.28 ± 0.062	1.49 ± 0.011	1.48 ± 0.018
50-100	0.98 ± 0.018 a	0.99 ± 0.056 a	1.17 ± 0.021 b	1.22 ± 0.028 b
100-200	0.66 ± 0.010	0.73 ± 0.053	0.97 ± 0.012	0.92 ± 0.014

NITROGEN

soil depth(cm)	campo limpo	campo sujo	cerrado aberto	cerrado denso
0-10	0.288 ± 0.005 a	0.211 ± 0.028 b	0.205 ± 0.003 b	0.226 ± 0.003 b
10-20	0.239 ± 0.006 a	0.146 ± 0.012 b	0.171 ± 0.004 b	0.172 ± 0.003 b
20-30	0.171 ± 0.006 a	0.121 ± 0.010 b	0.136 ± 0.004 b	0.136 ± 0.004 b
30-50	0.124 ± 0.007 a	0.077 ± 0.003 b	0.093 ± 0.005 b	0.091 ± 0.003 b
50-100	0.079 ± 0.002 a	0.048 ± 0.002 b	0.071 ± 0.003 a	0.071 ± 0.004 a
100-200	0.049 ± 0.001	0.038 ± 0.004	0.046 ± 0.002	0.049 ± 0.002

SULFUR

soil depth(cm)	campo limpo	campo sujo	cerrado aberto	cerrado denso
0-10	0.013 ± 0.0003 a	0.015 ± 0.0017 ab	0.033 ± 0.0009 c	0.019 ± 0.0012 b
10-20	0.013 ± 0.0005 a	0.013 ± 0.0027 a	0.020 ± 0.0005 b	0.013 ± 0.0007 a
20-30	0.012 ± 0.0002 a	0.015 ± 0.0015 a	0.018 ± 0.0007 b	0.012 ± 0.0004 a
30-50	0.011 ± 0.0003 ab	0.014 ± 0.0017 b	0.019 ± 0.0012 c	0.009 ± 0.0004 a
50-100	0.017 ± 0.0013 a	0.015 ± 0.0003 a	0.017 ± 0.0010 a	0.009 ± 0.0003 b
100-200	0.013 ± 0.0004 a	0.016 ± 0.0021 ab	0.019 ± 0.0012 b	0.008 ± 0.0002 c

Numbers are means followed by standard error. Different letters denote significant differences (P-value ≤ 0.10) when testing among communities using LSD test.

campo sujo soils through the 2.00 m depth, were between 0.013 and 0.016 %. In contrast, S concentrations in cerrado denso soils followed the same pattern as C and N, decreasing from surface to the deep areas of the soil. Sulfur concentrations in the upper 10 cm of the soil increased from campo limpo to cerrado aberto (0.013 % to 0.033 %), but declined in cerrado denso (Table 4.3.).

Along the Cerrado vegetation gradient, total C soil pool increased from 210,775 kg ha^{-1} to 256,992 kg ha^{-1} (Table 4.1.). Campo sujo had the lowest soil C mass and was the only community that differed significantly from the others (Table 4.1.). Campo limpo had the highest amount of total N in soil; from campo sujo to cerrado denso, total N increased from 12,150 kg ha^{-1} to 15,091 kg ha^{-1}. Total soil pool of S increased from campo limpo to cerrado aberto. However, total S pools were the lowest in cerrado denso.

Surface soil layers (0-10, 10-20, and 20-30 cm) of campo limpo tended to have a significantly higher C mass than other communities. For each depth interval up to 50 cm, soil N mass in campo limpo was significantly higher than campo sujo, cerrado aberto or cerrado denso. Cerrado aberto had the highest soil S pools for each depth interval. At 0-10 cm interval, cerrado aberto S pool was 308 kg ha^{-1}; the same soil interval at cerrado denso had 174 kg ha^{-1}.

Carbon and N mass decreased with soil depth (Table 4.1.). Carbon and N mass in the first meter of soil contributed to more than 62 % of the total soil pool in Cerrado s.l.. Campo limpo in the first meter contained 70 % of the total soil C and 71 % of the total soil N. In contrast, S mass was equally distributed throughout the soil profile. The upper 1.00 m of the soil profile comprised 51 %, 46 %, 49 % and 49 %, respectively, of the total mass in campo limpo, campo sujo, cerrado aberto and cerrado denso (Table 4.1.).

Total ecosystem C, N, and S pool

Total ecosystem nutrient pools (aboveground, root, and soil) did not have the same variability among communities as did aboveground and root nutrient pools. Total ecosystem pool ranged from 229,500 to 293,341 kg ha^{-1} of C, 12,450 to 17,720 kg ha^{-1} of N, and 1,566 to 3,753 kg ha^{-1} of S in campo limpo and cerrado denso respectively (Table 4.1.). Soil pools accounted for more than 86 % of all nutrients measured in all communities while roots comprised 0.3 to 8.7 %, and aboveground contained only 0.1 to 4.4 % of the total ecosystem pool (Figure 4.1.).

In terms of plant nutrient pools, most of the nutrient mass was in belowground components (Figure 4.2.). Root N and C pools were more than 80 % of the total aboveground and root pools combined for grasslands and more than 65 % of these combined pools for woodlands. Sulfur root pool in campo limpo also had 80 % of its total plant pool, but in campo sujo it dropped to 63 %. Cerrado aberto and cerrado denso tended to accumulate more S in the aboveground pool than did the other communities, with roots accounting for 53 % and 58 % respectively. Consequently, root:shoot ratios of nutrients were in generally higher for C and N than for S (Figure 4.2.). Carbon root:shoot ratio was approximately 4 in grasslands and 2 in woodlands. Nitrogen root:shoot ratio pool in campo limpo was 8, but decreased to 2 in woodlands. Sulfur root:shoot ratio was generally half of N root:shoot for all communities.

Fire effects on nutrients

Aboveground nutrient pools after fire included residual uncombusted material such as green graminoids, dicots, stems from shrubs, trees, and ash. Cerrado aberto and

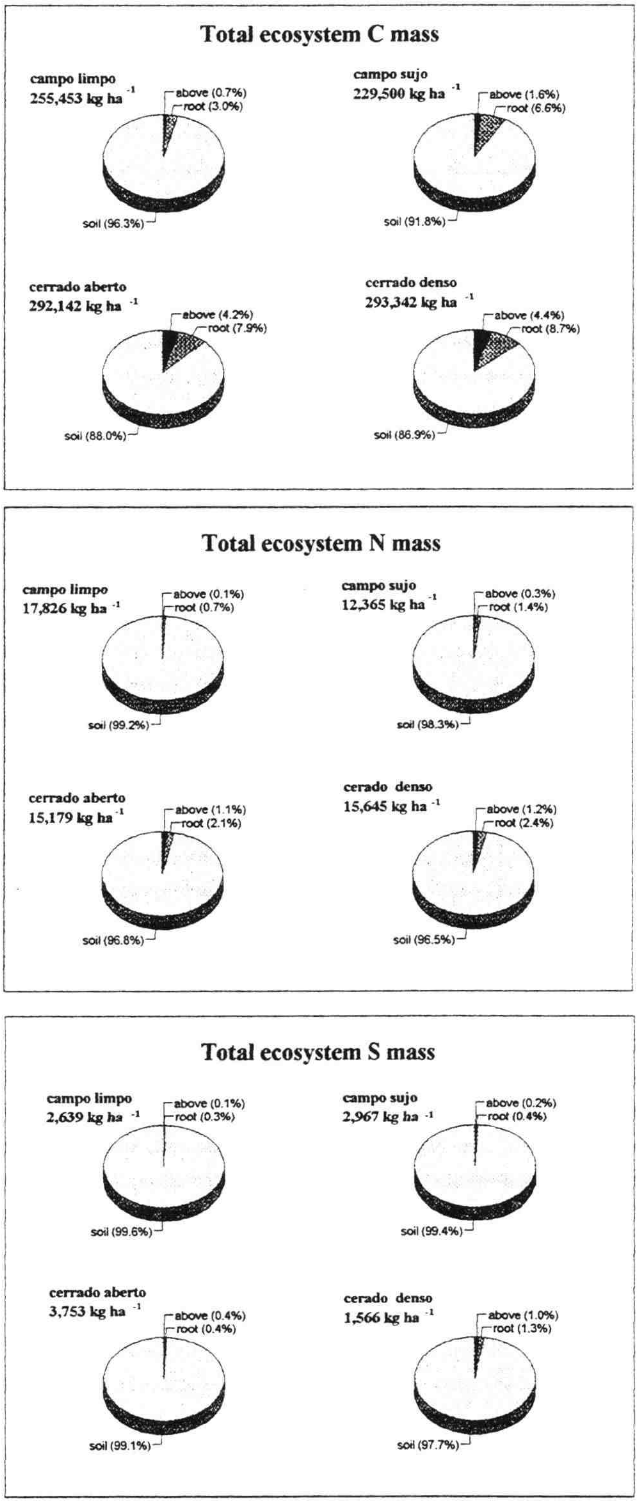


Figure 4.1. Relative proportion of carbon, nitrogen, and sulfur of the total ecosystem pool (above, root and soil) in Cerrado gradient, near Brasilia, DF, Brazil.

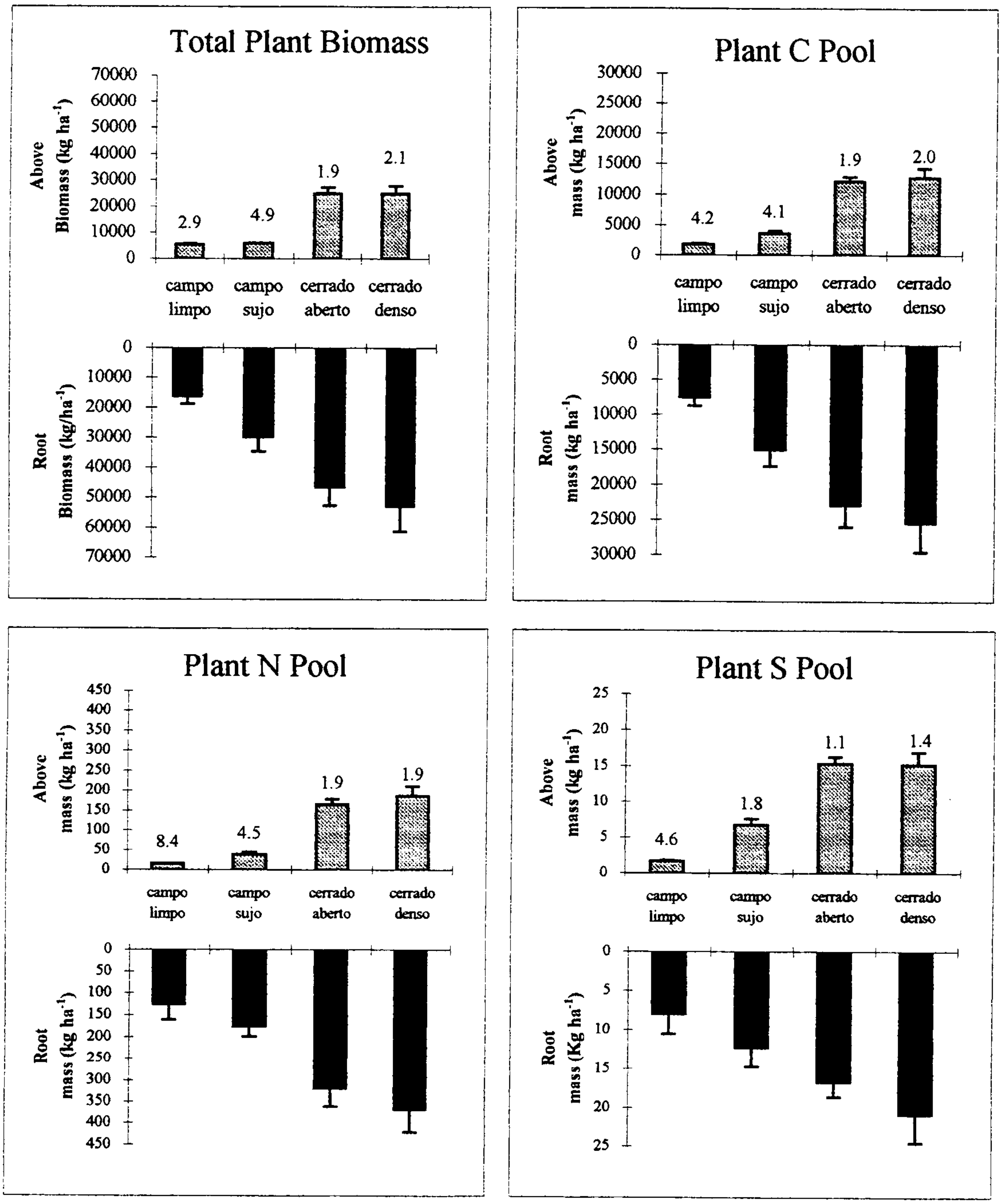


Figure 4.2. Comparison of aboveground biomass and root pools of carbon, nitrogen, and sulfur in Cerrado *sensu lato*. Bars are standard errors, and values above them are root:shoot ratio of biomass and nutrient masses.

cerrado denso had the highest mass of nutrients left on the ground after fire. Carbon nutrient pool after fire varied from 159 to 9,425 kg ha^{-1}, N nutrient pool after fire ranged from 2.2 kg ha^{-1}in campo limpo to 152 kg ha^{-1}in cerrado denso, and S pool after fire was between 0.1 kg $ha^{-1}$and 10.1 kg ha^{-1} in campo limpo and cerrado denso respectively (Figure 4.3.).

Nutrient concentration in ash increased from grasslands (20.6 % for C; 0.37 % for N, and 0.032 % for S) to woodlands; cerrado aberto had a slightly higher ash nutrient concentration (40.8 % for C, 1.15 % for N, and 0.057 % for S) than cerrado denso (Table 4. 4.A). Ash nutrient mass in cerrado aberto was greater than in other communities for all nutrients (Table 4. 4.B). Ash C mass in cerrado aberto was 928 kg ha^{-1}; N was 26.2 kg ha^{-1}; and S, 1.3 kg ha^{-1}. However, the percentage of loss by volatilization in cerrado aberto was the lowest of all communities, i.e. 81.6 % C, 34.6 % N, and 80.6 % S (Table 4.4.B). In contrast, campo limpo had the highest loss by volatilization of C (95.2 %), N (89.5 %), and S (91.4 %).

In terms of the total ecosystem, losses of nutrients by volatilization were minimal. Carbon losses in campo limpo were 0.67 %, in campo sujo 1.58 %, in cerrado aberto 1.61 %; and in cerrado denso 1.08 %. Nitrogen losses were 0.07 % for campo limpo, 0.20 % for campo sujo, 0.11 % for cerrado aberto, and 0.13 % for cerrado denso. Losses of S in campo limpo were 0.05 %, in campo sujo 0.19 %, in cerrado aberto 0.15 %, and in cerrado denso 0.25 %.

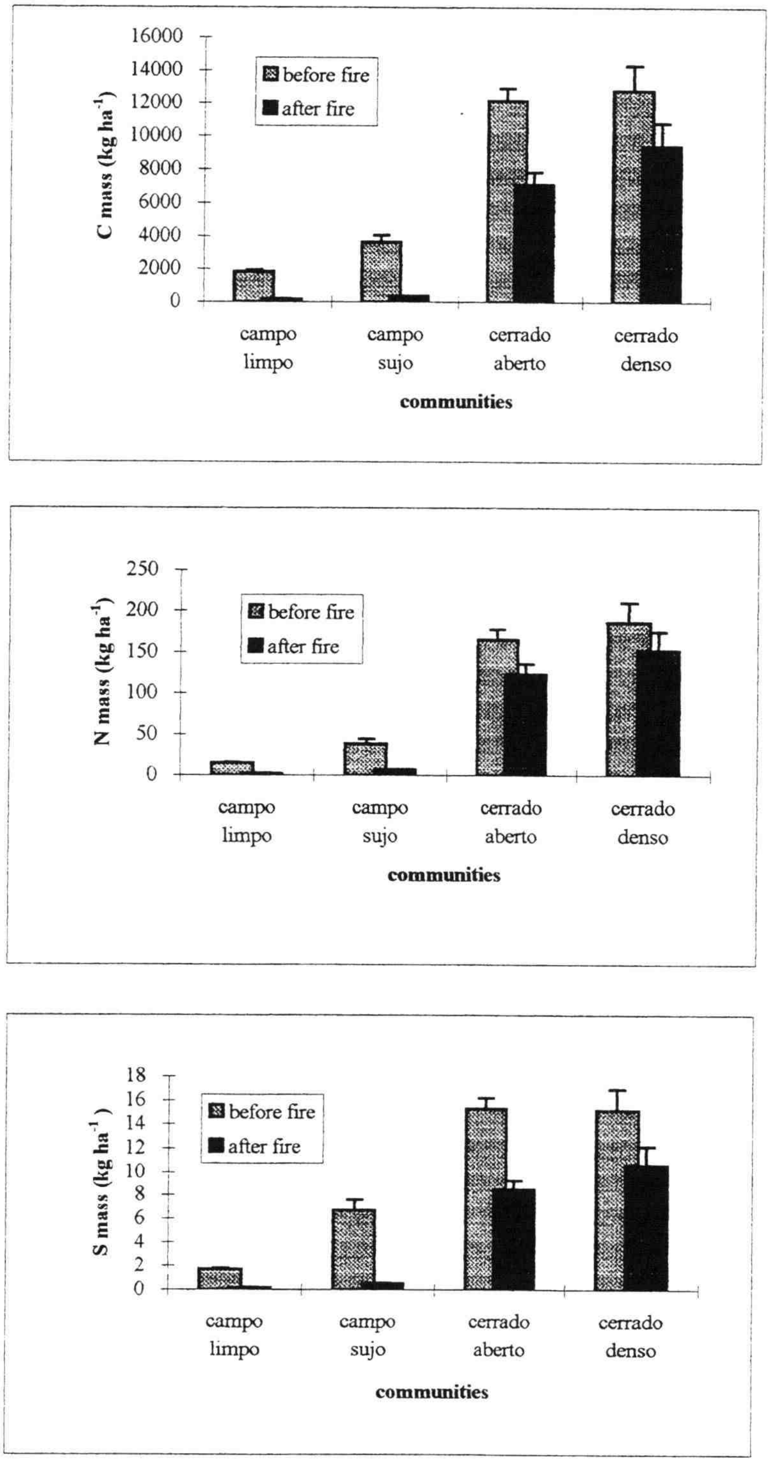


Figure 4.3. Aboveground carbon, nitrogen, and sulfur mass (kg ha^{-1}) in plant communities along a vegetation gradient in Cerrado *sensu lato* before and after fire, Brasilia, DF, Brazil.

Table 4.4. Nutrient ash concentration (%) (A), and total nutrient losses (B) via particulate transport and through volatilization (kg ha^{-1}) during fires along a vegetation gradient of Cerrado *sensu lato*, near Brasilia, DF, Brazil.

(A)

	campo limpo	campo sujo	cerrado aberto	cerrado denso
Carbon	20.65 ± 1.18	24.66 ± 1.25	40.83 ± 0.66	40.66 ± 1.34
Nitrogen	0.34 ± 0.03	0.55 ± 0.04	1.15 ± 0.03	1.00 ± 0.02
Sulfur	0.03 ± 0.00	0.04 ± 0.00	0.06 ± 0.00	0.05 ± 0.00

(B)

	campo limpo	campo sujo	cerrado aberto	cerrado denso
CARBON				
total site loss	1724.5 ± 117.4	3637.4 ± 413.5	5059.3 ± 175.4	3365.7 ± 309.3
particulate	83.1 ± 6.9	316.4 ± 28.3	928.3 ± 124.8	605.1 ± 59.7
volatilization	1641.4 ± 113.7	3321.0 ± 413.5	4131.0 ± 219.5	2760.6 ± 291.2
% loss volatilization	95.2 ± 0.4	90.9 ± 1.3	81.6 ± 2.6	81.7 ± 2.1
NITROGEN				
total site loss	12.9 ± 0.9	31.5 ± 5.8	42.0 ± 3.9	34.1 ± 2.2
particulate	1.4 ± 0.1	7.1 ± 0.6	26.2 ± 3.5	14.9 ± 1.5
volatilization	11.6 ± 0.9	24.4 ± 5.9	15.8 ± 6.6	19.2 ± 2.1
% loss volatilization	89.5 ± 0.8	74.7 ± 5.3	34.6 ± 12.8	56.2 ± 3.9
SULFUR				
total site loss	1.5 ± 0.1	6.2 ± 0.9	6.8 ± 0.4	4.6 ± 0.4
particulate	0.1 ± 0.0	0.5 ± 0.0	1.3 ± 0.2	0.7 ± 0.1
volatilization	1.4 ± 0.1	5.7 ± 0.9	5.5 ± 0.4	3.9 ± 0.4
% loss volatilization	91.4 ± 0.7	91.2 ± 1.8	80.6 ± 2.8	84.3 ± 1.5

Discussion

Aboveground pools

The increasing mass of aboveground nutrient pools along the gradient campo limpo to cerrado denso was associated with an increase in aboveground biomass (Chapter 2). The different structure of plant communities resulted in differences in total nutrient storage and within components of each community. The dominance of shrubs and trees in cerrado aberto and cerrado denso resulted in significant aboveground pools that did not exist in grasslands. This diversity of vegetation structure may influence the fire effects on the dynamic of nutrient pools.

Nutrient dynamics in Cerrado s.l. are poorly studied (Pereira 1982). Nitrogen mineralization in Cerrado is higher in the rainy season than during the dry season. Microbial activity increases with the higher soil humidity, increasing the rate of decomposition, and consequently the release of nutrients (Suhett et al. 1987). In the interval between natural fires in tropical savannas in general, decomposition although slow may be significant in increasing nutrient availability, particularly at the onset of the rainy season. (Frost and Robertson 1985, Swift et al. 1979). Therefore, the nutrient content in dead material (woody debris, litter and dry graminoids, and dead roots) is the primary source of plant available nutrients via decomposition (Vitousek and Sanford 1986). When fires occur in this ecosystem, most of the accumulated dead material is consumed (Chapter 2) and nutrients are released. In this study, dead material comprised the second highest relative proportion of the nutrient pool (after trees) (Table 4. 1.). After fire, most of these nutrients may be returned to the same site via ash deposition.

Few studies in Cerrado s.l. have investigated nutrient pools in aboveground biomass. Nitrogen and sulfur mass in the ground layer biomass (excluding shrubs and trees) ranges from 12.0 to 32.5 kg ha^{-1} and 2.6 to 6.8 kg ha^{-1}, respectively, in campo cerrado (Pivello and Coutinho 1992). These values are low compared to nutrient pools of the ground layer in cerrado aberto (64 kg ha^{-1} of N and 7.1 kg ha^{-1} of S) or cerrado denso (51.0 kg ha^{-1} of N and 5.7 kg ha^{-1} of S) of this study. The difference between literature values and those reported here are due to different methodologies used. I included materials from shrubs and trees in the litter component, and also quantified woody debris. For the ground layer of campo sujo, Batmanian and Haridasan (1985) reported a mass of 24 kg ha^{-1} of N for unburned area and 15 kg ha^{-1} of N for burned area. These values are also low compared to the 39 kg ha^{-1} measured in this study.

Carbon, N, and S mass of fuel of Cerrado s.l. were quantified by Kauffman et al. (1994). They reported nutrient pools of the fuel load to be approximately 3,350 kg ha^{-1} of C for grasslands and 4,500 kg ha^{-1} of C for woodlands. Nitrogen fuel load pool estimations is 25 kg ha^{-1} and 49 kg ha^{-1} for grassland and woodland, respectively. Sulfur fuel load is 3.7 kg ha^{-1} in grasslands and 5.6 kg ha^{-1} in woodland. The fuel load found in this study is in the range of those reported values. Fuel load in campo limpo and campo sujo for C, N, and S were the same as total nutrient pool because all components in these communities were very susceptible to fire. Cerrado aberto and cerrado denso had 5,942 kg ha^{-1} and 4,626 kg ha^{-1} of C, and 72 kg ha^{-1} and 55 kg ha^{-1} of N, respectively. Sulfur fuel load was 8 kg ha^{-1} for cerrado aberto and 10 kg ha^{-1} for cerrado denso.

Aboveground carbon, nitrogen, and sulfur pools in Cerrado s.l. were very low compared with either tropical rain forest or tropical dry forest. In the Brazilian Amazon forest, C, N, and S aboveground pools range from 148 to 218 Mg ha^{-1} of C, 1,401 to 2,327 kg ha^{-1} of N, and 251 to 392 kg ha^{-1} of S (Kauffman et al. 1995). In Amazon state, Klinge (1976) found 2,430 kg ha^{-1} of N in the aboveground biomass of tropical rain forest. In contrast, aboveground pools in this study were 13 Mg ha^{-1} of C, 185 kg ha^{-1} of N, and 15.2 kg ha^{-1} of S in the cerrado denso community, which had the highest nutrient pool in Cerrado s.l.. The Brazilian tropical dry forest, (known as caatinga) also had larger aboveground nutrient pools than Cerrado s.l.. The aboveground C pool in tropical dry forest is 34 Mg ha^{-1}, and aboveground N pool is 538 kg ha^{-1}(Kauffman et al. 1993). In addition , tropical dry forest in Puerto Rico has 368 kg ha^{-1} of N in the living parts of aboveground biomass (Lugo and Murphy 1986).

Root nutrient concentration and mass

Fine roots were expected to have the highest nutrient concentration, since their function is water and nutrient absorption, while the function of coarse roots is to conduct water, to support the plant and to store water and nutrients (Kerfoot 1963). The absence of a pattern such as the smaller the diameter the higher the nutrient concentration could be due to the diversity of species composition with variability in nutrient concentrations (Edwards and Grubb 1982), or to the contamination of fine roots by mineral soil and residual mycorrhiza that remained in the sample (Berish 1982).

Higher concentration of nutrients in tubers may be related to the occurrence of xylopodium (Chapter 3). In earlier studies, the function of these subterranean organs was believed to be water storage (Rawtscher and Rachid 1946 cited in Rizzini and Heringer 1961). However, more recently, Coutinho (1978c) demonstrated that water content in xylopodium was relatively low and constant throughout the year, while nutrient concentration was high, but variable. Peak of N concentrations in tubers of *Lantana montevidensis* (Verbenaceae) and *Isostigma peucedanifolium*, typical species of Cerrado s.l., were 1.9 % and 1.0 %, respectively. I found a range of 0.56 % to 1.23 % for N for the tubers measured in this study (Table 4.2.).

Prior to this study, no data were available for root nutrient pools in Cerrado s.l., and only a few studies of root nutrient pools had been reported for other tropical ecosystems (Klinge 1975, 1976, Edwards and Grubb 1982, Jordan et al. 1982, Lugo and

Murphy 1986). In tropical dry forest, root N pool is 546 kg ha^{-1} to a depth of 0.85 m (Lugo and Murphy 1986). For tropical moist forest in the Brazilian Amazon, root N pool is 404 kg ha^{-1} to a depth of 0.90 m (Klinge 1975). These amounts are larger than those found for Cerrado s.l. in this study. Here, N mass in roots up to 2.00 m deep ranged from 127 kg ha^{-1} in campo limpo to 369 kg ha^{-1} in cerrado denso. However, N mass in these roots of grassland communities comprised 80 % of phytomass nitrogen pool (aboveground and root), and 65 % in woodlands. In contrast, roots of tropical dry forest stored 45 % of the total plant N pool, while roots in tropical moist forest comprise only 19 % the total plant N pool (Klinge 1975, Lugo and Murphy 1986).

The distribution of nutrient masses among root diameters and tubers was more diversified in cerrado denso than in campo limpo. This is likely due to the increase of plant structural diversity in the cerrado denso community. Campo limpo and campo sujo still had tubers, which were probably from herbs. The nutrient masses in tubers of grasslands were lower because tuber biomass and concentration of nutrients were lower in these communities .

Carbon pools in tropical ecosystems have received more attention recently because of increases in atmospheric CO_2 and the potential role of these ecosystems as a source. Although root biomass may constitute a high portion of C storage, studies have neglected this pool because there is no immediate or readily observable release of C from belowground when land is cleared and burned (Brown and Lugo 1993). However, when a natural ecosystem is cut and burned for agricultural conversion, nutrient losses occur not only from the direct losses of fire, but also from erosion and release via microbial decomposition of dead roots (Vitousek 1983). Moreover, fine roots comprised 29 to 56 % of the total root mass (Chapter 2). After fire, this component of the root pool would be expected to disappear rapidly via decomposition.

Most of the carbon allocated and stored in roots may be used under conditions of stress such as drought, following fire or excessive grazing (Mooney 1972). This adaptation facilitates the existence of Cerrado vegetation in a nutrient-poor soils with frequent fires.

Soil nutrient concentration and mass

The higher concentration of C and N nutrients located in the upper horizons of the soil profile is likely related to higher concentrations of organic matter. Since decomposition results in deposition of organic residues on the soil surface, organic matter tends to accumulate in upper horizons and decrease with depth (Stevenson 1986, Brady 1990). However, S concentration in this study did not decrease as C and N did, except in cerrado denso. In weathered soils, such as in the Cerrado, the abundance of oxides of Fe and Al tend to adsorb SO_4^{-2} particularly at greater depths where the pH is suppose to higher (Barrow 1960, Couto and Ritchey 1987, Schlesinger 1991).

Campo limpo communities are associated with hydromorphic soils, which are poorly drained (Haridasan 1990), with medium to high clay contents of low activity, low pH, with a high concentration of aluminum (Furley and Ratter 1988). High water content and poor aeration may reduce the rate of decay, thereby, accumulating organic matter, which in turn may contribute to the higher concentration of total C and total N in the soil (Stevenson 1986, Brady 1990). In contrast, campo sujo, campo cerrado, and cerrado s.s. are associated with Oxisols (Haridasan 1990), which are deep, weathered, porous, and sometimes associated with surface organic matter (Furley and Ratter 1988). Since these soils are more favorable to the decomposition than are hydromorphic soils, oxidation of nutrients are faster and part of the nutrient readily available to plants. Nutrient concentration from campo sujo to cerrado s.s. has been discussed by Goodland and Pollard (1973). They found an increase in nutrient concentrations from campo sujo to cerrado s.s.. Lower sulfur concentration in campo limpo may be related with the anaerobic soil conditions for at least part of the year. Under these conditions, decomposition is slow, and produces different final products because different microorganisms are involved. Sulfur in gaseous form (H_2S) is one of the final products that is lost to the atmosphere (Stevenson 1986), possibly accounting for lower soil S concentration in campo limpo.

Pools of N in campo limpo soils were the highest due to higher N concentration in these communities. Moreover, bulk density in campo limpo was also one of the highest, especially in the first 0.30 m of the soil. Carbon and N pools decreased with depth as a function of lower nutrient concentration and lower soil bulk density (Appendix 4.3). The higher mass of S in the deep soil (100-200 cm), which was approximately 50 % of total S soil mass, was due to the higher concentration of S discussed before.

Although carbon stocks in soil have been reported as three to four times that of the living vegetation (Schlesinger 1990), I found C soil pool to a depth to 0.10 m to be 2 to 23 times more than aboveground biomass. The soil C pool in tropical rain forests in the states of Pará and Rondonia, in Brazil are estimated between 28 Mg ha^{-1} and 30 Mg ha^{-1} up to 10 cm in depth, respectively, or 11 to 17 % of the soil and aboveground combined (Kauffman et al. 1995). In the first 10 cm of Cerrado s.l. soils, C pool was 43 Mg ha^{-1} for campo limpo, 28 Mg ha^{-1} for campo sujo, 31 Mg ha^{-1} for cerrado aberto, and 32 Mg ha^{-1} for cerrado denso. Although the range of the soil C pool in Cerrado s.l. was similar to that reported for tropical rain forest (except for campo limpo), this top 10 cm of soil C corresponded to 95 % to 98 % of Cerrado s.l. aboveground biomass and soil combined. Considering that all these stored C is in balance with natural losses in the system (Perry et al. 1991), deforestation of Cerrado for agricultural purpose may release all these C by accelerating decomposition of organic matter in the soil, which will increase CO_2 in the atmosphere.

Fire effects on nutrient pools

Fire influences nutrient cycles by changing nutrient forms, nutrient distribution, and the mass of nutrients in the ecosystem (McNabb and Cromack Jr. 1990). The magnitude of these transformations depend upon fire intensity, fire duration, biomass nutrient content, and its consumption by fire (Frost and Robertson 1985), which in turn are related to vegetation structure. Woodlands had the highest masses of nutrients remaining after fire, most of which were bounded in unburned trees and shrubs. In contrast, campo limpo and campo sujo containing very combustible material, had low aboveground pools after fire.

High percentages of C, N, and S are lost via volatilization because they have low temperatures of volatilization (Kauffman et al. 1992). Nitrogen volatilizes at approximately 400 °C, which is lower than most fire temperatures registered for Cerrado s. l. (Cesar 1980, Miranda et al. 1993). Biomass consumption was not as complete for woodlands as for grasslands, which may have contributed to a lower loss by volatilization in woodlands, particularly cerrado aberto, compared to other communities. In addition, ash mass was high for cerrado aberto (Chapter 2, Table 2.1.) and consequently a higher nutrient mass was deposited in ash. Low concentrations of C, N, and S found in ash mass relative to plant tissue concentrations for all communities suggest that volatilization of those nutrients was high (Table 4.4.). Campo limpo and campo sujo, which contained highly combustible components, had the highest losses of nutrients via volatilization, because more of the fuel bed was consumed during flaming combustion than in the cerrado *sensu stricto* community. These patterns of loss are similar to those reported by Kauffman et al. (1994) where volatilization and relative amount of loss were high.

Losses of nutrients associated with fire in the Brazilian rain forest were much higher than in Cerrado s.l.. In this study, losses of C by volatilization ranged from 1,641 to 4,131 kg ha^{-1}, losses of N ranged from 11.6 to 24.4 kg ha^{-1}, and losses of S were between 1.4 to 5.7 kg ha^{-1}. Nutrient losses by fires in slashed primary tropical rain forest was between 58,000 and 112,000 kg $ha^{-1}$of C, 816 and 1,605 kg $ha^{-1}$of N, and 92 and 137 kg $ha^{-1}$of S (Kauffman et al.1995). These correspond to losses of 17 times more C, 24 times more N and 13 times more S in one burning of slashed primary tropical rain forest than losses in Cerrado s.l..

Total ecosystem C, N, and S pool

The distribution of the nutrient pool in Cerrado s.l., is unique relative to other tropical ecosystems. The high proportion of nutrient stocks found belowground is unlike that of moist and dry tropical forest. For example, total N pool in lowland tropical rain forest, in Brazil is 7,537 kg ha^{-1} 37 % of which is found in living aboveground biomass and litter, only 7 % in roots, and 56 % in soils (0-30 cm) (Klinge 1975 cited in Edwards and Grubb 1982). Tropical dry forest in Puerto Rico has 10,279 kg ha^{-1} of N in the total ecosystem. Aboveground biomass accounts for 6 %, roots 5 %, and soils 89 % (Lugo and Murphy 1986). Cerrado *sensu lato* in this study differed from the lowland tropical forest in the high amounts of nutrients in the soil (> 86 %), and much lower nutrient pool in the aboveground pool (0.1 to 8.7 %). Differences between this study and studies of tropical dry forest reported here is that, although tropical dry forest hold high nutrient pools in the soil, N is equally distributed in the phytomass; Cerrado *sensu lato* root biomass contributed to a greater pool of nutrients. This can be interpreted as an adaptative strategy for nutrient conservation in a nutrient-poor ecosystem with frequent fires.

Total ecosystem nutrient losses by fire were minimal because of the larger nutrient pools in the belowground part of the system. Belowground nutrient pools are well protected against disturbance such as fire. Soil is not strongly affected by fire because it has a low thermal conductivity. Slight increases in soil temperature were detected only in the top first 5 cm of soils during fires in Cerrado s.l. (Coutinho 1978a, Miranda et al. 1993). Fire influences on soil nutrient pools were negligible because temperatures do not get high enough to volatilized C, N, or S.

Nutrient root:shoot ratio in Cerrado *sensu lato* indicates an efficient nutrient conservation from fires, except for S in the woodlands, where half of its S pool was subject to consumption by fire. This may account for the low S pool in the whole ecosystem.

Conclusion

Estimation of total C, N, and S pool and fire effects discussed in this study are not available elsewhere for Cerrado *sensu lato*. Here, aboveground, root and soil nutrient pools of four community types ranging from grasslands to woodland were quantified in area near Brasilia, DF, Brazil.

In contrast to other tropical ecosystems, aboveground biomass of Cerrado s.l. contributed only a small percentage (≤ 4 %) of the total nutrient pools. Therefore, emissions of C, N and S to the atmosphere during burning were much lower than those reported for tropical rain or dry forest. In Cerrado s.l., the upper 10 cm of soil contains more than 90 % of the above and belowground nutrient pool. The large root mass contains for most of the nutrients stored in above and belowground plant biomass.

Deforestation in Cerrado s.l. may promote the release of a large mass of nutrients bounded in the root tissues and in the soil. The release of belowground C and other nutrients has not been included in the estimates of potential increases in atmosphere greenhouse gasses. Since, Cerrado s.l. has a large area in Brazil, and tropical savannas occupies 1530 million ha of the world land surface (Lanly 1982 cited in Andreae 1991), this potential sink or source of C and other nutrients can not be neglected.

Reference

Alvim, P. T., and W. A. Araujo. 1952. El suelo como factor ecológico en el desarollo de la vegetacion en el centro-oeste del Brasil. Turrialba 2:153-160.

Andreae, M.O. 1991. Biomass burning: Its history, use, and distribution and its impact on environmental quality and global climate. Pages 1-52 in J. S. Levine, editor. Global Biomass Burning: Atmospheric, Climatic, and Biospheric Implications

Barrow, N. J. 1960. A comparison of the mineralization and sulfur from decomposing organic materials. Australian Journal of Agriculture Research 11:960-969.

Batmanian, G. J. 1983. Efeitos do fogo sobre a produção primária e a acumulação de nutrientes no estrato rasteiro de um cerrado. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Batmanian, G. J., and M. Haridasan. 1985. Primary production and accumulation of nutrients by the ground layer community of cerrado vegetation of central Brazil. Plant and Soil 99:437-440.

Berish, C. W. 1982. Root biomass and surface area in three successional tropical forests. Canadian Journal Forestry Research 12:699-704.

Brady, N. C. 1990. The Nature and Properties of Soils, Tenth Edition . MacMillan Publishing Company, New York.

Brown, J. K., and A. E. Lugo. 1993. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8-18.

Cavalcanti, L. de H. 1978. Efeitos das cinzas resultantes da queima sobre a produtividade do estrato herbaceo-subarbustivo do cerrado de Emas (SP). Ph.D. Dissertation. Universidade de São Paulo, São Paulo.

Cesar, H. L. 1980. Efeitos da queima e corte sobre a vegetação de um campo sujo na fazenda Água Limpa, Distrito Federal. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Coutinho, L. M. 1977. Aspectos ecológicos do fogo no cerraod.II As queimadas e a dispersão de sementes em algumas especies anemocóricas do estrato herbaceo subarbustivo. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Botânica 5:57-64.

Coutinho, L. M. 1978a. Aspectos ecológicos do fogo no cerrado. I A temperatura do solo durante as queimadas. Revista Brasileira de Botânica 1:93-97.

Coutinho, L. M. 1978b. O conceito de cerrado. Revista Brasileira de Botânica 1:17-23.

Coutinho, L. M. 1979. Aspectos ecológicos do fogo no cerrado. III - A precipitação atmosférica de nutrientes minerais. Revista Brasileira de Botânica 2:97-101.

Coutinho, L. M. 1981. Aspectos ecológicos do fogo no cerrado - Nota sobre a ocorrência e datação de carvões vegetatis encontrados no interior do solo, em Emas, Pirassununga,SP. Revista Brasileira de Botânica 4:115-117.

Coutinho, L. M. 1990. Fire in the ecology of the Brazilian cerrado. Pages 82-105 in J. G. Goldammer, editor. Fire in the Tropical Biota- Ecosystem Process and Global Challenges. Volume 84. Springer Berlag, Berlin.

Coutinho, L. M., S. N. Pagano, and A. A. Sartori. 1978. Sobre o teor de água e nutrients minerais em xilopodios de algumas especies de cerrado. Ciência e Cultura 30 (Suplemento):349 pp.

Couto, W., and K. D. Ritchey. 1987. Enxofre. Pages 223-236 in W. J. Goedert, editor. Solos dos Cerrados - Tecnologias e estratégias de manejo, Primeira edição Edition. Editora Nobel, Brasilia,DF.

Crutzen, P.J., and M.O Andreae. 1990. Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles. Science 250:1669-1678

Dias, B. F.de S. 1990. Conservação da natureza no Cerrado brasileiro. Pages 583-640 in M. N. Pinto, editor. Cerrado: caracterização, ocupação e perspectivas. Editora da UnB, Brasilia.

Edwards, P. J., and P. J. Grubb. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil charactheristics and the division of mineral elements between the vegetation and soil. Journal of Ecology 70:649-666.

Eiten, G. 1972. The cerrado vegetation of Brazil. Botanical Review 38:201-341.

Frost, P. G. H., and F. Robertson. 1985. The ecological effects of fire in savannas. Pages 93-140 in B. H. Walker, editor. Determinants of Tropical Savannas. IRL Press Limited, Oxford.

Furley, P. A., and J. A. Ratter. 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. Journal of Biogeography 15:97-108.

Goodland, R. J. A. 1971. A physiognomy analysis of the "cerrado" vegetation of Central Brazil. Journal of Ecology 59:411-419.

Goodland, R., and R. Pollard. 1973. The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology 61:219-224.

Haridasan, M. 1990. Solos do Distrito Federal. Pages 309-330 in M. N. Pinto, editor. Cerrado: Caracterização, ocupação e perspectivas. Editora da UnB, Brasilia.

Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. Journal of Ecology 82:519-531.

Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: Biomass, nutrient pools, and losses in slashed primary forests. in press.

Kauffman, J. B., R. L. Sanford Jr., D. L. Cummings, I. H. Salcedo, and E. V. S. B. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74(1):140-151.

Kauffman, J. B., K. M. Till, and R. W. Shea. 1992. Biogeochemistry of deforastation and biomass burning. Pages 426-456 in D. A. Dunnette and R. J. O'Brien, editors. The Science of Global Change: The impact of human activities on the Environment, Americal Chemical Society Symposium Edition. Volume Series 483. American Chemnical Society, Washington,DC.

Kerfoot, O. 1963. The root systems of tropical forest trees. Commonwealth Forestry Review 42:19-26.

Klinge, H. 1975. Root mass estimation on lowland tropical rain forests of central Amazonian, Brazil.I. Nutrietns in fine roots from giant humus podzols. Tropical Ecology 16:28-38.

Klinge, H. 1976. Root mass estimation in lowland tropical rain forests of central Amazonia, Brazil. IV. Nutrients in fine roots from Latosols. Tropical Ecology 17(79):79-88.

Lofgren, A. 1898. Ensaio para uma distribuição dos vegetais nos diversos grupos floristicos no estado de São Paulo. Boletim Comissão Geografica e Geologia de São Paulo 11:1-50.

Lopes, A., and F. R. Cox. 1977. Cerrado vegetation in Brazil: an edaphic gradient. Agronomy Journal 69:828-831.

Lugo, A. E., and P. G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. Journal of Tropical Ecology 2:55-72.

McNabb, D. H., and K. Cromack Jr. 1990. Effects of prescribed fire on nutrients and soil productivity. Pages 125-142 in J. D. Walstad, S. R. Radosevich and D. V. Sandberg, editors. Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State Press, Corvallis, OR.

Miranda, A. C., H. S. Miranda, I. de F. O. Dias, and B F. de S. Dias. 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. Journal of Tropical Ecology 9:413-431.

Mooney, H. A. 1972. The Carbon Balance of Plants. Annual Review of Ecology and Systematics 3:315-346.

Pereira, J. 1982. Nitrogen cycling in South American savannas. Plant and Soil 67:293-304.

Peres, J. R. R., A. R. Suhet, M. A. T. Vargas, and A. Drozdowicz. 1983. Litter production in areas of Brazilian "Cerrados". Boletim de Pesquisa Agropecuaria Brasileira 18(9):1037-1043.

Perry, D. A., J. G. Borchers, D. P. Turner, S. V. Gregory, C. R. Perry, R. K. Dixon, S. C. Hart, J. B. Kauffman, R. P. Neilson, and P. Sollins. 1991. Biological feedbacks to climate change: Terrestrial ecosystems as sinks and sources of carbon and nitrogen. The Northwest Environmental Journal 7:203-232.

Pivello, V. R., and L. M. Coutinho. 1992. Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). Journal of Tropical Ecology 8:487-497.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Canadian Journal of Forest Research 15:132-140.

Ramos, A. E. 1990. Efeitos da queima sobre a vegetação lenhosa do cerrado. Tese de Mestrado. Universidade de Brasilia (Brasilia, DF).

Raw, A., and J. D. Hay. 1985. Fire and other factors affecting population of Simarouba amara in cerradao near Brasilia, Brazil. Revista Brasileira de Botânica 8:101-107.

Rizzini, C. T., and E. P. Heringer. 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phyton 17(1):105-124.

Rosa, C. M. M. 1990. Recuperação pos fogo do estrato rasteiro de um campo sujo de cerrado. Tese de Mestrado. Universidade de Brasilia, Brasilia, DF.

Schlessinger, W. H. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature 348:232-234.

Schlessinger, W. H. 1991. Biogeochemestry: an analysis global change. Academic Press,Inc., San Diego, California.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, second Edition. W, H, Freeman and Company, New York.

Stevenson,F. J. 1986. Cycles of soil - Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients. Wiley Interscience Publication - John Wiley & Sons, New York.

Suhet, A. R., J. R. R. Peres, and M. A. T. Vargas. 1987. Nitrogenio. Pages 167-202 in W. J. Goedert, editor. Solos do Cerrado - Tecnologia e estratégias de manejo, Primeira edição Edition. Editora Nobel, Brasilia.

Swift, M. J., O. W. Heal, and J. M. Anderson, editors. 1979. Decomposition in Terristerial Ecosystem. Volume Studies in Ecology, 5. Blackwell, London.

Vitousek, P. M. 1983. The Effects of Deforestation on Air, Soil, and Water. Pages 223-245 in B. Bolin and R. B. Cook, editors. The Major Biogeochemical Cycles and Their Interactions. Volume SCOPE 21. John Wiley & Sons, Chichester.

Vitousek, P. M., and R. L. Sanford Jr. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137-167.

Warming, E., and M. Ferri. 1973. Lagoa Santa e a Vegetação de Cerrados Brasileiros. Editora da USP and Editora Itatiaia, São Paulo.

CHAPTER 5
CONCLUSION

Cerrado *sensu lato*, a tropical savanna, increased in aboveground and root biomass from grassland to woodland. These results suggested that each community type of the Cerrado gradient may be characterized by its biomass, in addition to the classification by tree density and basal area(Goodland and Pollard 1973), species composition (Eiten 1972) or plant physiognomy and structure(Eiten 1972, Coutinho,1976).

Roots accounted for most of the aboveground and root biomass combined, resulting in an ecosystem with a very high root:shoot ratio. Consequently, Cerrado *sensu lato* had a large pool of nutrients in its phytomass, even though nutrient concentrations were low. However, nutrient pools in the root are at least twice greater than aboveground pools for C and N.

Natural disturbances, such as fire, affect the ecosystem level by accelerating nutrient cycling and energy flow (White and Pickett 1985). Biomass consumption promotes nutrient volatilization, an emission of particulates that may contribute to the increase of CO_2 in the atmosphere as well the greenhouse effect.

Cerrado *sensu lato* vegetation has been characterized as very well adapted to fire (Coutinho, 1990). It has been described as a low severity fire regime with a fire return interval between 1-2 years for grasslands and 3-5 years for woodland (Eiten 1975, Pivello and Coutinho 1992).

This study indicates that nutrient pools are distributed in the total ecosystem of Cerrado *sensu lato* so that even with frequent fires, most of the nutrients remain in the ecosystem. The majority of nutrients are in the belowground systems (soil and root), which are not affected by fire. Consequently, emissions of C and other nutrients to the atmosphere from biomass burning in Cerrado *sensu lato* are much lower than in any other tropical ecosystem of the same extended area. Nevertheless, considering the extensive area of the world covered by tropical savannas and the frequency of fires, the total amount of C and other nutrients released into the atmosphere by the many individual fire may be substantial.

However, the low price of the land combined with the facilities of a mechanized agriculture is changing the Cerrado *sensu lato* landscape in the central part of Brazil. Monoculture of soybeans, rice, corn and eucalyptus is displacing the natural vegetation. Deforestation of Cerrado *sensu lato* may promote a release of nutrients stored in the roots and in the soil. Although, release of these nutrient through farming is not immediate and much slower than nutrient release by biomass burning, nutrient losses is still considerable. These losses need to be considered in the models of global climate change to insure that predictions will be as accurate as possible.

Bibliography

Ab'Saber, A. N. 1983. O dominio dos cerrados: introdução ao conhecimento. Revista do Servidor Publico 111(4):41-55.

Adamoli, J., J. Macedo, L. G. de Azevedo, and J. M. Netto. 1987. Caracterização da região dos Cerrados. Pages 33-75 in W. J. Goedert, editor. Solos dos Cerrados: Tecnologia e estratégias de manejo, Primeira edição Edition. Editora Nobel, Brasilia.

Agee, J. K. 1990. The historical role of fire in Pacific Nortwest forests. Pages 25-38 in J. D. Walstad, S. R. Radosevich and D. V. Sandberg, editors. Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis,OR.

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:349-357.

Alho, C. J. R. 1990. Distribuição da fauna num gradiente de recursos em mosaico. Pages 205-256 in M. N. Pinto, editor. Cerrado: Caracterização, Ocupação e Pespectivas, Primeira edição Edition. Editora da UnB, Brasilia,DF.

Alvim, P. T., and W. A. Araujo. 1952. El suelo como factor ecologico en el desarollo de la vegetacion en el centro-oeste del Brasil. Turrialba 2:153-160.

Anderson, A. B., and D. A. Posey. 1987. Reflorestamento indigina. Ciência Hoje 31:44-50.

Andreae, M. O. 1991. Biomass burning: Its history, use, and distribution and its impact on environmental quality and global climate. Pages 1-52 in J. S. Levine, editor. Global Biomass Burning: Atmospheric, Climatic, and Biospheric Implications. The MIT Press, Cambridge.

Askew, G. P., D. J. Moffatt, R. F. Montgomery, and P. L. Searl. 1970. Interrelationships of soil and vegetation in the Savanna-forest boundary zone of north-eastern Mato Grosso. Geographical Journal 136:370-376.

Askew, G. P., D. J. Moffatt, R. F. Montgomery, and P. L. Searl. 1971. Soils and soil moisture as factors influencing the distribution of the vegetation formations of the Serra do Roncador, Mato Grosso. Pages 150-170 in M. G. Ferri, editor. III Simposio sobre o cerrado. Editora Edgard Blucher Ltda & Editora da Universidade de São Paulo, São Paulo. (N)

Barrow, N. J. 1960. A comparison of the mineralization and sulfur from decomposing organic materials. Australian Journal of Agriculture Research 11:960-969.

Batmanian, G. J. 1983. Efeitos do fogo sobre a produção primária e a acumulação de nutrientes no estrato rasteiro de um cerrado. Tese de Mestado. Universidade de Brasilia, Brasilia, DF.

Batmanian, G. J., and M. Haridasan. 1985. Primary production and accumulation of nutrients by the ground layer community of cerrado vegetation of central Brazil. Plant and Soil 99:437-440.

Berger, R., and W. F. Libby. 1966. UCLA Radiocarbon Dates V. Radiocarbon 8:467-497.

Berish, C. W. 1982. Root biomass and surface area in three successional tropical forests. Canadian Journal Forestry Research 12:699-704.

Blydenstein, J. 1962. La sabana de Trachypogon del alto llano. Boletin de la Sociedade Venezolana de Ciencias Naturales 102:139-206.

Blydenstein, J. 1967. Tropical savanna vegetaiton of the Llanos of Colombia. Ecology 48:1-15.

Bohn, W. 1979. Methods of studying root systems. Springer-Verlag, New York.

Bolin, B., E. T. Degens, S. Kempe, and P. Ketner. 1979. The global biogeochemical carbon cycle. Pages 1-56 in B. Bolin, E. T. Degens, S. Kempe and P. Ketner, editors. The Glogal Carbon Cycle. John Wiley & Sons, Chichester.

Bourliere, F., and M. Hardley. 1983. Present-day savannas: an overview. Pages 1-17 in F. Bourliere, editor. Tropical Savannas - Ecosystems of the World. Volume 13. Elservier Scentific Publishing Company, Amestrdam.

Brady, N. C. 1990. The Nature and Properties of Soils, Tenth Edition. MacMillan Publishing Company, New York.

Brown, A. A., and K. P. Davis. 1973. Forest Fire: Control and Use. Mcgraw-Hill Company, New York.

Brown, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. Forest Science 17(1):96-102.

Brown, J. K., and P. J. Roussopoulos. 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. Forest Science 14:350-356.

Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with application to forest inventory data. Forest Science 35(4):881-902.

Brown, S., and A. E. Lugo. 1993. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8-18.

Castellanos, J., M. Maass, and J. Kummerow. 1991. Root biomass of a dry decidous tropical forest in Mexico. Plant and Soil 131:225-228.

Cavalcanti, L. H. 1978. Efeito das cinzas resultantes da queimada sobre a produtividade do estrato herbaceo subarbustivo do cerrado de Emas. Tese de Livre Docência. Universidade de São Paulo, São Paulo.

Cesar, H. L. 1980. Efeitos da queima e corte sobre a vegetação de um campo sujo na fazenda Água Limpa, Distrito Federal. Tese de Mestado. Universidade de Brasilia, Brasilia, DF.

Chandler, C., P. Cheney, P. Thomas, L. Trabaud, and D. Williams. 1983. Fire in the Forest - Forest Behavior and Effects. Volume 1. John Wiley & Sons, New York.

Coutinho, L. M. 1976. Contribuição ao conhecimento do papel ecológico das queimadas na floração de especies do cerrado. Livre Docente Tese. Universidade de São Paulo, São Paulo, SP.

Coutinho, L. M. 1977. Aspectos ecológicos do fogo no cerraod.II As queimadas e a dispersão de sementes em algumas especies anemocóricas do estrato herbaceo subarbustivo. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Botânica 5:57-64.

Coutinho, L. M. 1978a. Aspectos ecológicos do fogo no cerrado. I A temperatura do solo durante as queimadas. Revista Brasileira de Botânica 1:93-97.

Coutinho, L. M. 1978b. O conceito de cerrado. Revista Brasileira de Botânica 1:17-23.

Coutinho, L. M. 1979. Aspectos ecológicos do fogo no cerrado. III - A precipitação atmosférica de nutrientes minerais. Revista Brasileira de Botânica 2:97-101.

Coutinho, L. M. 1981. Aspectos ecológicos do fogo no cerrado - Nota sobre a ocorrência e datação de carvões vegetais encontrados no interior do solo, em Emas, Pirassununga,SP. Revista Brasileira de Botânica 4:115-117.

Coutinho, L. M. 1982. Ecological effects of fire in Brazilian cerrados. Pages 273-291 in B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savannas. Volume 42. Springer-Verlag, Berlin. (N)

Coutinho, L. M. 1984. Aspectos ecológicos do fogo no cerrado. A sauva, as queimadas e sua possivel relação na ciclagem de nutrientes minerais. Boletim da Faculdade de Filosofia e Ciências da Universidade de São Paulo, Zoologia 8:1-9.

Coutinho, L. M. 1990. Fire in the ecology of the Brazilian cerrado. Pages 82-105 in J. G. Goldammer, editor. Fire in the Tropical Biota- Ecosystem Process and Global Challenges. Volume 84. Springer Berlag, Berlin.

Coutinho, L. M., Y. S. De Vuono, and J. S. Lousa. 1982. Aspectos ecológicos do fogo no cerrado. A época da queimada e a produtividade primária líquida epigéia do estrato herbaceo subarbustivo. Revista Brasileira de Botânica 5:37-41.

Coutinho, L. M., S. N. Pagano, and A. A. Sartori. 1978. Sobre o teor de água e nutrients minerais em xilopodios de algumas especies de cerrado. Ciência e Cultura 30 (Suplemento):349 pp.

Couto, W., and K. D. Ritchey. 1987. Enxofre. Pages 223-236 in W. J. Goedert, editor. Solos dos Cerrados - Tecnologias e estratégias de manejo, Primeira edição Edition. Editora Nobel, Brasilia,DF.

Crutzen, P. J., and M. O. Andreae. 1990. Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles. Science 250:1669-1678.

Deeming, J. E., R. E. Burgan, and J. D. Cohen. 1977. The National fire danger rating system. USDA Forest Service General Technical Report INT-39.Ogden,UT.

Dias, B. FdeS. 1990. Conservação da natureza no Cerrado brasileiro. Pages 583-640 in M. N. Pinto, editor. Cerrado: Caracterização, Ocupação e Perspectivas. Editora da UnB, Brasilia.

DNER-Departamento Nacional de Estradas de Rodagem. 1976. Classificação climatica de Wladimdir Koppen, Reimpressão Edition. Servico de Publicação, Rio de Janeiro.

Edwards, P. J., and P. J. Grubb. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil charactheristics and the division of mineral elements between the vegetation and soil. Journal of Ecology 70:649-666.

Eiten, G. 1972. The cerrado vegetation of Brazil. Botanical Review 38:201-341.

Eiten, G. 1975. Vegetation of the Serra do Roncador. Biotropica 7:112-135.

Eiten, G. 1978. Delimitation of the cerrado concept. Vegetatio 36:169-178.

Eiten, G. 1992. How names are used for vegetation. Journal of Vegetation Science 3:419-424.

Fearnside, P. M. 1992. Greenhouse gas emissions from deforestation in the Brazilian Amazon. in W. Makundi and J. Sathaye, editors. Carbon emissions and sequestration in forests: case studies from seven developing countries, Draft Edition. Volume 2. U.S. Environmental protection Agency, Climate Change Division, Washington, DC and Energy and Environment Division,Lawrence Berkeley Laboratory, Berkeley, CA, .

Felfili, J., and M. C. da Silva Jr. 1993. A comparative study of cerrado (sensu stricto) vegetation in Central Brazil. Journal of Tropical Ecology 9:277-289.

Filgueiras, T. S., S. E. David, and F. O. Zuluoga. 1993. Ophiochloa, a new endemic serpentine grass genus (Poaceae:Paniceae) from the Brazilian Cerrado vegetation. Novon 3(4):360-366.

Fisher, M. J., I. M. Rao, M. A. Ayarza, C. E. Lascano, J. I. Sanz, R. J. Thomas, and R. R. Vera. 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. Nature 371:236-238. Nature 371:236-238.

Frost, P. G. H., and F. Robertson. 1985. The ecological effects of fire in savannas. Pages 93-140 in B. H. Walker, editor. Determinants of Tropical Savannas. IRL Press Limited, Oxford.

Furley, F. A., and J. A. Ratter. 1988. Soil resources and plant communities of the central brazilian cerrado and their development. Journal of Biogeography 15(1):97-108.

Gibbs, P. E., H. F. Leitao Filho, and G. Shephered. 1983. Composition and community structure in an area of Cerrado in SE Brazil. Flora. Morphologie, Geobotanik, Okologie 173:433-449.

Gillon, D. 1983. The fire problem in tropical savannas. Pages 617-641 in F. Bourliere, editor. Tropical Savannas. Volume Ecosystems of the World no.13. Elsevier Scientific Publishing Company, Amesterdan.

Goedert, W. J. 1983. Management of the Cerrado soils of Brazil: a review. Journal of Soil Science 34:405-428.

Goodland, R. J. A. 1971. A physiognomy analysis of the "cerrado" vegetaiton of Central Brazil. Journal of Ecology 59:411-419.

Goodland, R., and M. G. Ferri. 1979. Ecologia do Cerrado. Livraria Itatiaia Editora Ltda, Belo Horizonte,MG.

Goodland, R., and Pollard. 1973. The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology 61:219-224.

Greeland, D. J., and J. M. L. Kowal. 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12(2):154-173.

Haridasan, M. 1990. Solos do Distrito Federal. Pages 309-330 in M. N. Pinto, editor. Cerrado: Caracterização, Ocupação e Perspectivas. Editora da UnB, Brasilia.

Harris, W. F., P. Sollins, N. T. Edwards, B. E. Dinger, and H. H. Sugharet. 1972. Analysis of carbon flow and productivity in a temperate deciduous forest ecosystem. Pages 116-122 in D. E. Reichle, J. F. Franklin and D. W. Goodwall, editors. Productivity of World Ecossytem. National Academyof Science, Washington, DC.

Heringer, E. P., G. M. Barroso, and J. A. Rizzo. 1977. A flora do Cerrado. Pages 211-232 in M. G. Ferri, editor. IV Simposio sobre o Cerrado. Universidade de São Paulo, São Paulo.

Hopkins, B. 1962. Vegetation of the Olokmeji Forest Reserve, Nigeria. I General features of the reserve and the researsh sites. Journal of Ecology 50:559-598.

Huntley, B. J. 1982. Southern african savannas. Pages 101-119 in B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savanas. Volume Ecological studies 42. Springer Verlag, Berlin.

Jesko, T. 1992. The root as an integral part of the plant. Pages 1-29 in J. Kolek and V. Kozinka, editors. Physiology of the Plant Root System. Volume Development in Plant and Soil Sciences, 46. Kluwer Academic Plublishers, Czechoslovakia. (N)

Jordan, C. F. 1985. Nutrient Cycling in Tropical Forest Ecosystems., Great Britain.

Jordan, C., W. Caskey, G. Escalante, R. Herrera, and F. Montagnini. 1982. The nitrogen cycle in a 'tierra firme' rain forest on oxisol on the Amazon Territory of Venezuela. Plant and Soil 67:325-332.

Jordan, C. F., and C. Uhl. 1978. Biomass of a "tierra firme' forest of the Amazon Basin. Oecologia Plantarum 13:387-400.

Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. Journal of Ecology 82:519-531.

Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: Biomass, nutrient pools, and losses in slashed primary forests. Ecology in press.

Kauffman, J. B., R. L. Sanford Jr., D. L. Cummings, I. H. Salcedo, and E. V. S. B. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74(1):140-151.

Kauffman, J. B., K. M. Till, and R. W. Shea. 1992. Biogeochemistry of deforastation and biomass burning. Pages 426-456 in D. A. Dunnette and R. J. O'Brien, editors. The Science of Global Change: The impact of human activities on the Environment, Americal Chemical Society Symposium Edition. Volume Series 483. American Chemnical Society, Washington,DC.

Kerfoot, O. 1963. The root systems of tropical forest trees. Commonwealth Forestry Review 42:19-26.

Klinge, H. 1975. Root mass estimation on lowland tropical rain forests of central Amazonian, Brazil.I. Nutrietns in fine roots from giant humus podzols. Tropical Ecology 16:28-38.

Klinge, H. 1976. Root mass estimation in lowland tropical rain forests of central Amazonia, Brazil. IV. Nutrients in fine roots from Latosols. Tropical Ecology 17(79):79-88.

Klinge, H., W. A. Rodrigues, E. Brunig, and E. J. Fittkau. 1975. Biomass and structure in a central Amazonian rain forest. Pages 398 in F. B. Golley and E. Medina, editors. Tropical Ecological Systems - Trends in Terrestrial and Aquatic Research. Volume Ecological Studies 11. Springer-Verlag, New York.

Lammotte, M. 1978. La savanne preforestiere de Lamto, Cote d'Ivore. Pages 231-311 in F. Bourliere and M. Lammotte, editors. Problems d'ecologie, structure et fonchonnment des ecosystemes terrestres., Masson, Paris.

Lawson, G. W., J. Jenik, and K. O. Armstrong-Mensah. 1968. A study of a vegetation catena in Guinea savanna ar Mole Game Reserve (Ghana). Journal of Ecology 56:505-522.

Lofgren, A. 1898. Ensaio para uma distribuição dos vegetais nos diversos grupos floristicos no estado de São Paulo. Boletim Comissão Geografica e Geologia de São Paulo 11:1-50.

Lopes, A., and F. R. Cox. 1977. Cerrado vegetaiton in Brazil: an edaphic gradient. Agronomy Journal 69:828-831.

Lugo, A. E., and P. G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. Journal of Tropical Ecology 2:55-72.

Magalhães, J. V. C. de. 1913. O Selvagem, Segunda Edition. Editora Livraria Itatiaia and Editora da Universidade de São Paulo, São Paulo.

McClung, A. C., and L. M. M. de Freitas. 1959. Sulfur deficiency in soils from Brazilian campos. Ecology 40(2):315-317.

McNabb, D. H., and K. Cromack Jr. 1990. Effects of prescribed fire on nutrients and soil productivity. Pages 125-142 in J. D. Walstad, S. R. Radosevich and D. V. Sandberg, editors. Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State Press, Corvallis, OR.

Menaut, J. C., and J. Cesar. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. Ecology:1197-1210.

Miranda, A. C., Miranda HS, I. de F. O. Dias, and B. F. de S. Dias. 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. Journal of Tropical Ecology 9:413-431.

Monk, C. 1966. Ecological importance of root/shoot ratios. Bulletin of the Torrey Botanical Club 93(6):402-406.

Mooney, H. A. 1972. The Carbon Balance of Plants. Annual Review of Ecology and Systematics 3:315-346.

Murphy, P. G., and A. E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18(2):89-96.

Nepstad, D. C. 1989. Forest regrowth in abandoned pastures of eastern Amazonia; limitations to tree seedling survival and growth. Ph.D. Dissertation. Yale University.

Nepstad, D. C., E. Amaral, I. F. Brown, C. Klink, G. Negreiros, M. Pedlowski, and C. Uhl. 1995. Land-usein Amazonia and the Cerrado of Brazil: Current status and trends. A white paper for the NASA/LBA Science Plan. Draft version. .

Oliveira-Filho, A. T. de, G. J. Shepherd, F. R. Martins, and W. H. Stubblebine. 1989. Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. Journal of Tropical Ecolcogy 5:413-431.

Pereira, J. 1982. Nitrogen Cycling in South American Savannas. Plant and Soil 67:293-304.

Peres, J. R. R., A. R. Suhet, M. A. T. Vargas, and A. Drozdowicz. 1983. Litter production in areas of Brazilian "Cerrados". Boletim de Pesquisa Agropecuaria Brasileira 18(9):1037-1043.

Perry, D. A., J. G. Borchers, D. P. Turner, S. V. Gregory, C. R. Perry, R. K. Dixon, S. C. Hart, J. B. Kauffman, R. P. Neilson, and P. Sollins. 1991. Biological feedbacks to climate change: Terrestrial ecosystems as sinks and sources of carbon and nitrogen. The Northwest Environmental Journal 7:203-232.

Pivello, V. R., and L. M. Coutinho. 1992. Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). Journal of Tropical Ecology 8:487-497.

Pyne, S. J. 1984. Introduction to Wildland Fire: Fire Management in the United States, 1st Edition. John Wiley & Sons, New York,NW.

Rachid-Edwards, M. 1956. Alguns dispositivos para proteção de plantas contra a seca e o fogo. Boletim da Faculdade de Filosofia, Ciências e Letras da USP 219 Botânica 13:37-69.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Canadian Journal of Forest Research 15:132-140.

Ramos, A. E. 1990. Efeitos da queima sobre a vegetação lenhosa do cerrado. Tese de Mestado. Universidade de Brasilia, Brasilia, DF.

Ratter, J. A., and T. C. D. Dargie. 1992. An analysis of the floristic composition of 26 cerrado areas in Brazil. Edinburgh Journal of Botany 49(2):235-250.

Raw, A., and J. D. Hay. 1985. Fire and other factors affecting population of Simarouba amara in cerradao near Brasilia, Brazil. Revista Brasileira de Botânica 8:101-107.

Rawitscher, F. 1948. The water economy of the vegetation of the campos cerrados in southern Brazil. Journal of Ecology 36(2):237-268.

Richards, J. H. 1986. Root form and depth distribution in several biomes. in C. Carlisle, W. L. Berry, I. R. Kaplan and Watterson, editors. Mineral exploration: Biological Systems and Organic Matter. Volume V. Prentice Hall, Englewood cliffs, New Jersey.

Rizzini, C. T. 1976. Tratado de Fitogeografia do Brasil. Volume I. Editora Hucitec e Editora da USP, São Paulo.

Rizzini, C. T., and E. P. Heringer. 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phyton 17(1):105-124.

Rizzini, C. T., and E. P. Heringer. 1962. Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. Anais da Academia Brasileira de Ciências 34:235-247.

Rosa, C. M. M. 1990. Recuperação pos fogo do estrato rasteiro de um campo sujo de cerrado. Tese de Mestado. Universidade de Brasilia, Brasilia, DF.

Rothermel, R. C., and J. E. Deeming. 1980. Measuring and interpreting fire behavior for correlation with fire effects. USDA-For. Serv. Gen. Tech. Rep.INT-93, Ogden,UT.

Russel, R. S. 1977. Plant root systems; their function and interaction with the soil. McGraw-Hill, London.

Sambuichi, R. H. R. 1991. Efeitos de longo prazo do fogo periódico sobre a fitossociologia da camada lenhosa de um cerrado em Brasilia, DF. Tese de Mestado. Unibersidade de Brasilia, Brasilia,DF.

Sanford Jr, R. L. 1989. Root systms of three adjacent, old growth Amazon forests and associated transition zones. Journal of Tropical Forest Science 1(3):268-279.

Santantonio, D., R. K. Hermann, and W. S. Overton. 1977. Root biomass studies in forest ecosystem. Pedobiologia 17:1-31.

Sarmiento, G. 1983. The savannas of tropical America. Pages 245-288 in F. Bourliere, editor. Tropical Savannas. Volume Ecosystems of the World - 13. Elsevier, Amsterdan.

Sarmiento, G., and M. Monasterio. 1975. A critical consideration of the environmental conditions associated with the ocurrence of savanna ecossytems in tropical America. Pages 223-250 in F. B. Golley and E. Medina, editors. Tropical Ecological Ecosystems. Springer-Verlag, Berlin.

Sarmiento, G., and M. Vera. 1979. Composicion, estructure, biomassa y produccion de differentes sabanas en los Llanos de Venezuela. Boletin de la Sociedade Venezolana de Ciencias Naturales 136:5-41.

Schlessinger, W. H. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature 348:232-234.

Schlessinger, W. H. 1991. Biogeochemestry: an analysis global change. Academic Press,Inc., San Diego, California.

Silberbauer, I., and G. Eiten. 1987. A hecatare of Cerrado. I. General aspects of the trees and thick-stemmed shrubs. Phyton 27(1):55-91.

Silva, J., M. Monasterio, and G. Sarmiento. 1971. Reconocimiento ecologico de los llanos Occidentales. II. El Norte del Estado de Barinas. Acta Cientifica Venozolana 22:60-71.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry - The Principles and Practice of Statistics in Biological Research, 2nd Edition. W.H. Freeman and Company, New York.

Stark, N., and M. Spratt. 1977. Root biomass and nutrient storage in Rainforest Oxisols near San Carlos de Rio Negro. Tropical Ecology(18):1-9.

Stevenson, F. J. 1986. Cycles of Soil - Carbon, Nitrogen, Phosphorus, Sulfur, micronutrients. Wiley Interscience Publication - John Wiley & Sons, New York.

Suhet, A. R., J. R. R. Peres, and M. A. T. Vargas. 1987. Nitrogenio. Pages 167-202 in W. J. Goedert, editor. Solos do Cerrado - Tecnologia e estratégias de manejo, Primeira edição Edition. Editora Nobel, Brasilia.

Swift, M. J., O. W. Heal, and J. M. Anderson, editors. 1979. Decomposition in Terristerial Ecosystem. Volume Studies in Ecology, 5. Blackwell, London.

Trollope, W. S. W. 1978. Fire Behavior - a preliminary study. Proceedings of the Grassland Society of Southern Africa 13:123-128.

Trollope, W. S. W. 1982. The ecological effects of fire in South African savannas. Pages 292-306 in B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savannas. Volume Ecological Studies 42. Springer Verlag, Berlin.

Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. Forest Science 14(1):20-26.

Van Wagner, C. E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research 3:373-378.

Vitousek, P. M. 1983. The Effects of Deforestation on Air, Soil, and Water. Pages 532 in B. Bolin and R. B. Cook, editors. The Major Biogeochemical Cycles and Their Interactions. Volume SCOPE 21. John Wiley & Sons, Chichester.

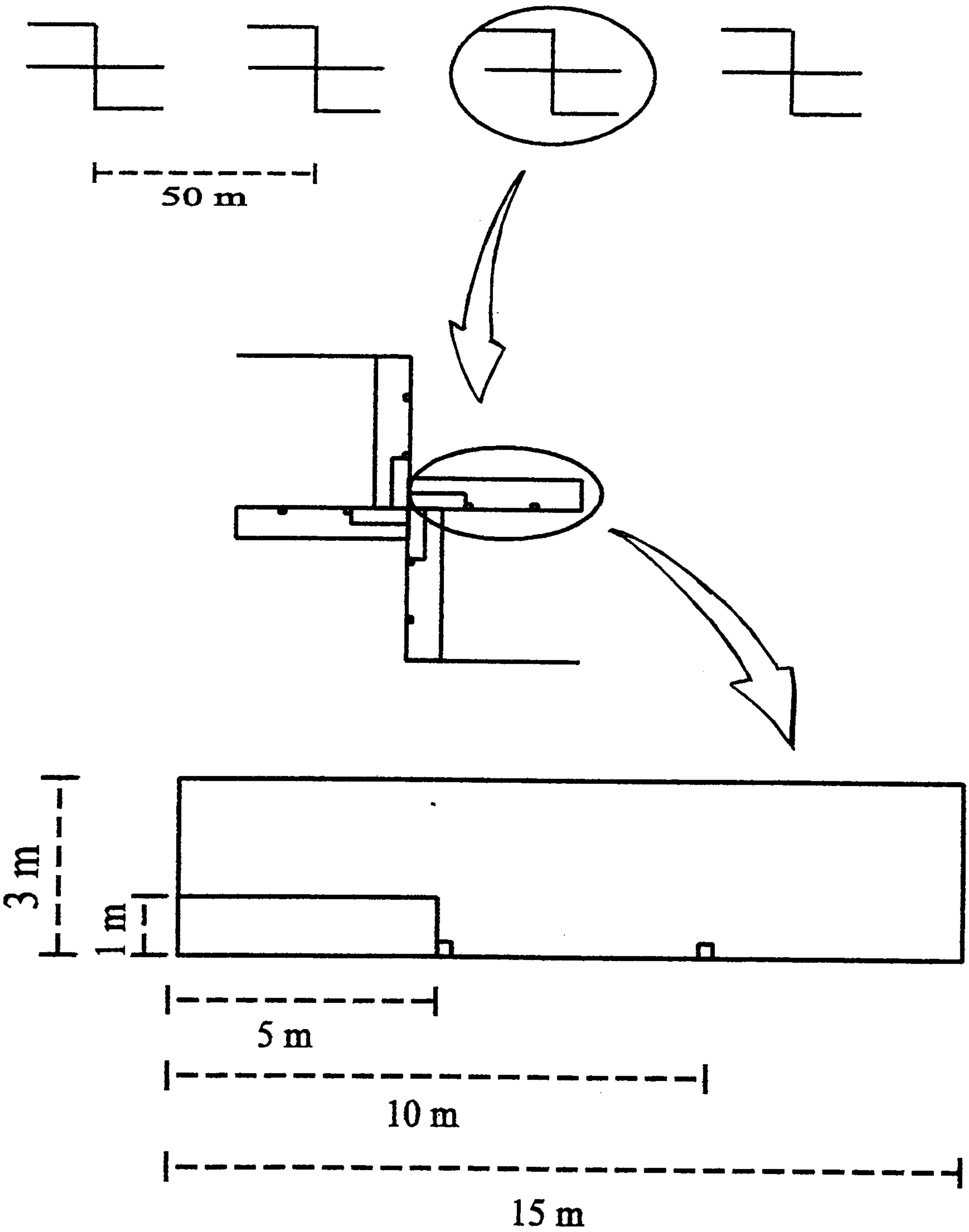
Vitousek, P. M., and R. L. Sanford Jr. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137-167.

Warming, E., and M. Ferri. 1973. Lagoa Santa e a Vegetação de Cerrados Brasileiros. Editora da USP and Editora Itatiaia, São Paulo.

White, P.S. and S. T. A. Pickett. 1985. Natural disturbances and patch dynamics; an introduction. Pages 3-13- The Ecology of Natural Disturbance and Patch Dynamics. Academic Press Inc.

APPENDICES

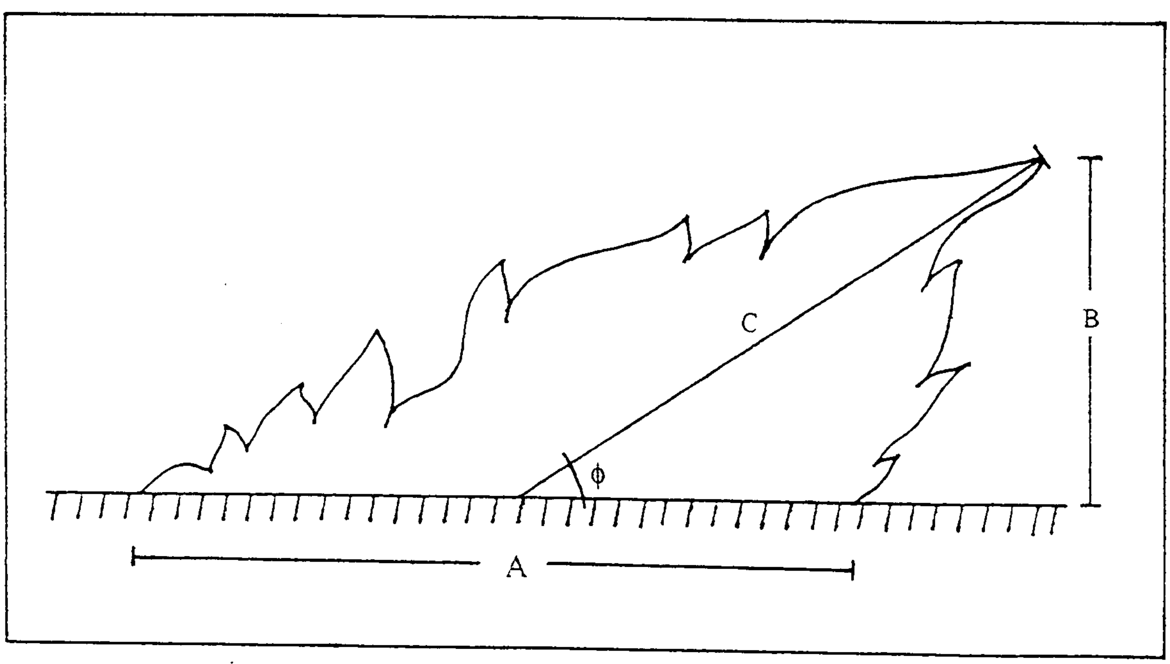
Appendix 2.1. Experimental design for aboveground biomass established at each community type of Cerrado *sensu lato*, Brasilia, DF, Brazil. Total sample sizes were 32 for herbs and graminoids, wood debris = 24, and shrubs and trees = 16.



Appendix 2.2. Multiple regression equations to estimate shrub biomass of Cerrado *sensu lato* at IBGE Ecological Reserve, Brasilia,DF. (N=35).(Source: Dr. B. Kauffman personal communication)

Dependent variable	Equation	R^2	AdjR^2
Total biomass (g)	721.404(Volume m^3)+8.4331(diameter mm)	.96	.95
Leaf biomass (g)	24.7801(Volume m^3)+51.5634(height m)	.82	.80

Appendix 3.2. Fire descriptors: A = flame depth, B = flame height, C = flame length and ϕ = flame angle.



Appendix 4.1. Nutrient concentration (%) of aboveground biomass along a vegetation gradient in Cerrado ecosystem, Reserva Ecologica, IBGE-Brazil. Numbers are mean and standard error. Numbers followed by a different superscription letter denote a significant difference (P<0.05) in concentration when testing between plant communities (Source: Kauffman et al. 1994).

Component	Campo limpo	Campo sujo	Campo cerrado	Cerrado *sensu stricto*
Carbon				
Wood debris < 0.64 cm in diameter	—	—	—	51.47 (0.14)
Wood debris ≥ 0.64 cm in diameter	—	—	—	51.87 (0.16)
Dicot litter	—	50.32 (0.53)^{a}	52.07 (0.38)^{b}	52.19 (0.46)^{b}
Dicots – prefire	—	49.03 (0.32)^{a}	51.78 (0.28)^{b}	52.04 (0.33)^{b}
Dicots – postfire	—	—	51.56 (0.12)	51.75 (0.27)
Live grass	47.89 (0.28)	47.77 (0.08)	47.84 (0.20)^{b}	47.34 (0.10)^{a}
Dormant grass	47.36 (0.11)^{ab}	47.10 (0.17)^{a}	47.71 (0.12)^{b}	47.06 (0.10)^{a}
Shrub leaves	—	—	53.19 (0.83)	53.96 (0.37)
Ash	22.50 (0.41)^{a}	24.81 (1.19)^{a}	50.88 (1.16)^{b}	52.62 (1.14)^{b}
Nitrogen				
Wood debris < 0.64 cm in diameter	—	—	—	0.532 (0.013)
Wood debris ≥ 0.64 cm in diameter	—	—	—	0.362 (0.043)
Dicot litter	—	0.704 (0.028)	0.722 (0.027)	0.752 (0.031)
Dicots – prefire	—	0.792 (0.037)	0.717 (0.083)	0.714 (0.075)
Dicots – postfire	—	—	0.495 (0.024)	0.447 (0.020)
Live grass	0.508 (0.017)^{a}	0.578 (0.024)^{ab}	0.647 (0.022)^{b}	0.535 (0.035)^{a}
Dormant grass	0.261 (0.009)^{a}	0.282 (0.009)^{a}	0.313 (0.012)^{b}	0.317 (0.011)^{b}
Shrub leaves	—	—	1.274 (0.033)	1.095 (0.080)
Ash	0.233 (0.011)^{a}	0.264 (0.011)^{a}	0.873 (0.027)^{b}	0.953 (0.023)^{c}
Sulfur				
Wood debris < 0.64 cm in diameter	—	—	—	0.044 (0.004)
Wood debris ≥ 0.64 cm in diameter	—	—	—	0.034 (0.004)
Dicot litter	—	0.073 (0.004)	0.083 (0.007)	0.080 (0.005)
Dicots – prefire	—	0.256 (0.156)	0.086 (0.011)	0.092 (0.004)
Dicots – postfire	—	—	0.069 (0.009)	0.067 (0.005)
Live grass	0.049 (0.003)^{a}	0.067 (0.003)^{b}	0.070 (0.066)^{b}	0.067 (0.003)^{b}
Dormant grass	0.039 (0.002)	0.034 (0.003)	0.036 (0.003)	0.038 (0.002)
Shrub leaves	—	—	0.135 (0.007)^{a}	0.109 (0.007)^{b}
Ash	0.102 (0.002)^{a}	0.063 (0.011)^{b}	0.062 (0.002)^{b}	0.056 (0.004)^{b}

Appendix 4.2. Nutrient concentration (%) of leaves and stems of Cerrado *sensu lato* trees (N = 5).

	carbon	nitrogen	sulfur
stems	53.62 ±0.58	0.686 ±0.07	0.05 ±0.00
leaves	52.36 ±0.23	1.114 ±0.16	0.07 ±0.00

Appendix.4.3. Bulk density (g cm^{-3}) up to 2.00 m in depth, in soils of Cerrado vegetation gradient, near Brasilia, DF, Brasilia.

Depth	campo limpo	campo sujo	cerrado aberto	cerrado denso
0-10	0.929 ± 0.052	0.958 ± 0.031	0.821 ± 0.035	0.810 ± 0.025
10-20	1.003 ± 0.027	1.097 ± 0.035	0.961 ± 0.019	0.916 ± 0.026
20-30	1.121 ± 0.007	1.120 ± 0.038	0.999 ± 0.016	1.005 ± 0.020
30-50	0.852 ± 0.044	1.103 ± 0.039	0.960 ± 0.015	0.990 ± 0.023
50-100	0.909 ± 0.032	0.985 ± 0.033	0.954 ± 0.007	0.927 ± 0.019
100-200	1.021 ± 0.067	1.086 ± 0.030	0.975 ± 0.027	0.983 ± 0.021