

## **Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire**

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**ABSTRACT.** Conversion to permanent agriculture is rapidly occurring over vast areas of the 1.8 million km<sup>2</sup> Brazilian Cerrado; a region that is naturally a mosaic of grasslands, savannas and evergreen tropical woodlands. Yet, few studies have quantified total biomass of plant communities in this ecosystem, particularly the belowground component; a C pool of potential global significance. Total biomass (aboveground and belowground), and the quantity of biomass consumed by fires were measured in four plant communities comprising a vegetation gradient from pure grassland (campo limpo) to a woodland with a closed canopy of tall shrubs and scattered trees (cerrado denso) near Brasilia, DF, Brazil. Total aboveground biomass (TAGB) increased along this gradient from 5.5 Mg ha<sup>-1</sup> in campo limpo to 29.4 Mg ha<sup>-1</sup> in cerrado denso. Vegetation structure varied among communities; trees were nonexistent in campo limpo, but were at a density of 1000 ha<sup>-1</sup> and a biomass of 12.9 Mg ha<sup>-1</sup> in cerrado denso. Fires consumed 92 and 84% of the TAGB in campo limpo (pure grassland) and campo sujo (savanna), respectively. In cerrado aberto and cerrado denso, trees and tall shrubs were little affected by fire. Combustion factors of the TAGB in these communities was 54 and 33%, respectively. The total biomass consumed by fire ranged from 5.0 Mg ha<sup>-1</sup> in campo limpo to 13.5 Mg ha<sup>-1</sup> in cerrado aberto. Compared to other widespread Brazilian ecosystems (tropical dry forest and evergreen forest), the Cerrado has a lower aboveground biomass. The TAGB of cerrado denso is <9% of that of Amazonian tropical evergreen forest. The total quantity of biomass consumed by fire, and hence emissions to the atmosphere is lower in intact Cerrado communities compared to fires in slashed tropical forest.

Total belowground biomass (TBGB) increased from 16.3 Mg ha<sup>-1</sup> in campo limpo, to 30.1 Mg ha<sup>-1</sup> in campo sujo, to 46.5 Mg ha<sup>-1</sup> in cerrado aberto, and to 52.9 Mg ha<sup>-1</sup> in cerrado denso. This quantity of belowground biomass is similar to, or exceeds that reported for many tropical dry and moist forests. More than 80% of the TBGB occurred in the upper 30 cm of the soil, except for cerrado denso (71%) where a greater proportion of tree roots were present at deeper levels. Root:shoot ratios were very high in all sites ranging from 2.9 in cerrado denso to 7.7 in campo sujo. Total ecosystem plant biomass (the total aboveground biomass and TBGB combined) ranged from 21.9 Mg ha<sup>-1</sup> in campo limpo to 77.9 Mg ha<sup>-1</sup> in

cerrado denso. More than 71% of the live phytomass (aboveground biomass + root biomass) is belowground in the Brazilian Cerrado. At current rates of land cover change in the Brazilian Cerrado, these ecosystem pools are likely significant sources of increasing atmospheric C and other greenhouse gasses.

**KEY WORDS:** aboveground biomass, Brazil, belowground biomass, Cerrado, fire ecology, fuels, root mass, tropical savana

#### INTRODUCTION

The Brazilian Cerrado is a tropical ecosystem containing a diverse mosaic of grasslands, savannas, woodlands and forests (Coutinho 1976). This ecosystem comprises 1.8 million km<sup>2</sup> in the central part of Brazil (Ab'Saber 1983), and fires and land conversion are widespread at present. However, few studies in the Cerrado have quantified total aboveground biomass (TAGB), or described the effects of fire in this ecosystem. Although the variability of fuel biomass, nutrient pools, fire behaviour and consumption in Cerrado communities were reported by Pivello & Coutinho (1992) and Kauffman *et al.* (1994), these studies did not include trees in their estimates of aboveground biomass.

In most ecosystems of the world, belowground structure and biomass have not received the same degree of study as the aboveground component (Russel 1977, Sanford 1989). This lack of information is related to the degree of difficulty and time associated with the methods of sampling, as well as the disturbance associated with destructive sampling approaches (Santantonio *et al.* 1977). Belowground tissues are poorly understood with respect to their function as ecosystem (and global) C pools. The relationship between increasing atmospheric CO<sub>2</sub>, climate change and accelerated rates of land use conversion in the tropics require better quantification of both the total aboveground and belowground biomass pools (Fearnside 1992). In tropical dry forests, total root biomass has been reported to range from 10 to 45 Mg ha<sup>-1</sup> (Castellanos *et al.* 1991, Murphy & Lugo 1986). In three different forest community types of tropical evergreen forest in the Venezuelan Amazon, Sanford (1989) reported root biomass to range from 55 to 61 Mg ha<sup>-1</sup>. In the eastern Amazon of Brazil (Para State), Nepstad (1989) found root biomass in an intact tropical rain forest and a degraded grass/shrub community to be 35 and 10 Mg ha<sup>-1</sup>, respectively. Murphy & Lugo (1986) reported a range in root biomass of 11–135 Mg ha<sup>-1</sup> for tropical wet forests. In savanna and savanna woodlands of Africa and South America root biomass has been reported to range from 12–37 Mg ha<sup>-1</sup>. Even though the Cerrado is the second largest vegetation type in Brazil comprising 23% of the country's land area (Eiten 1972) we could find no published studies where the belowground biomass of communities has been described.

The Brazilian Cerrado developed as a response to a history of frequent fires, nutrient poor soils, a deep water table, and a climate with marked wet and dry seasons (Eiten 1972). Eiten (1975) estimated the average frequency of fire set by indigenous people of the Cerrado in Mato Grosso, Brazil, to be 3–5 y. Among

the plant adaptations to these environmental variables are the presence of belowground meristematic and storage organs (Rachid-Edwards 1956, Rawitscher 1948; Rizzini & Heringer 1961, 1962). We predicted that in response to frequent fire, annual drought, and nutrient-poor soils, a greater portion of plant biomass in the Cerrado would be belowground, such that root biomass and root:shoot ratios would be high relative to other tropical ecosystems. If true, a relatively minor percentage of the plant biomass is exposed to natural ecosystem disturbances (e.g., natural fires), whereas all of the plant biomass (and related C and nutrient pools) could be affected by human perturbations (e.g., land use/land cover changes).

Given the areal extent of the Brazilian Cerrado, large scale anthropogenic perturbations could alter global source/sink dynamics of C and other greenhouse gasses. Klink *et al.* (1994) estimated that as of 1991, 600,000 km<sup>2</sup> of Cerrado had been cleared with an annual rate of 20 000 km<sup>2</sup> y<sup>-1</sup>. This exceeds the deforestation rates of the tropical evergreen forests of the Amazon (e.g., 230,000–415,000 km<sup>2</sup>; Fearnside 1992; Skole & Tucker 1993). An accurate assessment of aboveground and belowground biomass of intact Cerrado vegetation types is a necessary step in determining the consequences of land conversion on local, regional and global processes. To address this research need, we established the following objectives: (1) quantify total aboveground biomass before and after fire in four plant communities forming a common vegetation gradient consisting of grassland, savanna and woodlands; and (2) quantify total belowground biomass (TBGB), root distribution and root structure along this same gradient.

#### STUDY SITE

Research was conducted during the latter part of the dry season and early part of the wet season, 1993, at the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE) and the Jardim Botânico de Brasília (JBB). These sites are located *c.* 35 km south of Brasília, Brazil (15°51'S 47°63'W). The elevation is 1100 m and slopes are <10%. From 1980 to 1992, mean annual temperature varied from 19 to 22 °C. Mean precipitation was 1482 mm and distributed in two distinctive seasons; a wet season from October to March with a mean precipitation of 1257 mm and a dry season from April to September with a mean precipitation of 225 mm. Mean maximum relative humidity was 81% in December and the mean minimum was 55% in August (File data from Reserva Ecológica do IBGE 1980–1992).

The vegetation of the Brazilian Cerrado is characterized by five community types along a gradient of increasing dominance by woody species: campo limpo (pure grassland), campo sujo (a savanna with a sparse presence of shrubs), campo cerrado (a dominance of shrubs with scattered trees and a grass understorey), cerrado *sensu stricto* (a dominance of trees with scattered shrubs and a grass understorey), and cerradão (a closed canopy forest) (Coutinho

1978, Eiten 1972, Goodland & Pollard 1973). Within the common cerrado *sensu stricto* community, stands with a more open tree canopy are referred to as cerrado aberto and those with a more closed canopy as cerrado denso. In this study, biomass and fires were measured in campo limpo, campo sujo and in the two variants of Cerrado *sensu stricto* (cerrado aberto and cerrado denso). Cerrado *sensu stricto* and campo sujo communities are usually found on latosols (oxisols) and podzolic soils (alfisols or ultisols); campo limpo is associated with lithosols (lithic dystropepts) in the uplands and with hydromorphic soils (inceptisols) in low areas ecotonal to riparian zones and other wet areas (Haridasan 1990). Soils in all sites have low nutrient concentrations, high aluminum contents, and low pH.

#### METHODS

##### *Aboveground biomass*

Measurements of TAGB in this study included all living vegetation (phytomass) as well as dead vegetation (necromass). TAGB was partitioned into components based on plant morphology and their variable influences and responses to fire. All prefire sampling of TAGB occurred within 1 wk before burning and postfire TAGB was measured within 1 wk after fire. In each of the four sampled communities, four clusters of 15-m transects were established. Downed wood debris was quantified along six transects in each cluster ( $n = 24$  per community). Other components were measured in four transects in each cluster ( $n = 16$  per community). The first cluster was randomly established and the others were systematically established 50 m distant from each other. Aluminum stakes marked the ends of each 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 technique (Brown 1971, Brown & Roussopoulos 1974, Van Wagner 1968). This component was not present in the campo limpo and campo sujo grasslands. Dead wood was partitioned into diameter size classes based upon the following standard timelag classes: 0 to 0.64 cm in diameter (1-h timelag fuels), 0.65 to 2.54 cm in diameter (10-h timelag fuels), 2.55 to 7.6 cm in diameter (100-h timelag fuels) (Deeming *et al.* 1977). No wood  $>7.6$  cm in diameter ( $\geq 1000$ -h timelag fuels) was encountered in the plots. The timelag constant is the time period required for a wood fuel particle to lose 63% of its initial moisture content when placed in an equilibrium temperature of 27 °C and relative humidity of 20% (Pyne 1984). The 1-h timelag fuels were measured along the first 5 m of the transect; 10-h fuels were measured from 0 to 10 m and the 100-h fuels were measured along the entire 15 m transect. Biomass was calculated utilizing the formulas provided by Brown (1974) and adapted to the Cerrado by Kauffman *et al.* (1994). After fire, the transects were remeasured to quantify residual plant materials that were not consumed.

*Herbaceous stratum, litter and ash.* The herbaceous stratum contained hardwood litter, green and dry graminoids, terrestrial members of the Bromeliaceae and Palmae, and small dicots (defined as those <1.0 cm in diameter and/or those with main stems  $\geq$ 1.0 cm in diameter, but <0.50 m in height). All materials within a 25-cm  $\times$  25-cm microplot placed at the 5- and 10-m points along each transect were collected by clipping at the soil surface, and then oven-dried at 60 °C for 48 h to obtain dry-weight mass ( $n = 32$  plots per community). Samples from 10 microplots in each community were randomly selected for separation of the total biomass into the components listed above. The ratio of each component to the total mass was calculated through this separation. This specific ratio for each community was utilized to calculate mass of each component in each community. Post-fire mass of this layer was collected along each transect at 6- and 11-m points, employing the same methods as pre-fire sampling.

Ash mass was calculated through collection of all ash in a 50-cm  $\times$  50-cm plot placed at the 6-m point on each transect in each cluster ( $n = 16$ ). Ash was collected using a vacuum cleaner and electric generator.

*Shrubs.* All woody plants with a main stem  $\geq$ 1.0 cm in diameter, and with a height range of 0.5–2.0 m were measured in a 1-m  $\times$  5-m belt transect established adjacent to the transects. The height and elliptical crown area of all shrubs in each plot were measured. The elliptic crown area was calculated as the longest canopy diameter multiplied by the perpendicular diameter and  $\pi$  and then divided by four. Crown volume was calculated by multiplying elliptic crown area by height. Biomass of shrubs was calculated through multiple regression analysis with volume, stem diameter and height as independent variables. This model was developed based upon destructive sampling of 20 shrubs collected at the Ecological Reserve. After fire, plots were remeasured utilizing the same methods.

*Trees.* The diameter and height of all trees (>2.0 m in height) were measured in 3-m  $\times$  15-m plots established adjacent to the herbaceous and wood transects. Diameter measurements were taken at heights 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 (Felfili & Silva 1993, Ramos 1990, Sambuichi 1991, Silberbauer & Eiten 1987). However, equations used for the calculation of tree biomass were based on the diameter at 1.30 m. Tree density was also calculated from the transects. Tree biomass was calculated using the equation presented by Brown *et al.* (1989) for moist tropical forests. Although this equation was not developed specifically for Cerrado trees, it is believed to be very robust and the most applicable (Dr. S. Brown, US-EPA Corvallis OR U.S.A., *pers. comm.*). This study provides a preliminary estimate of tree biomass even though the accuracy of this biomass model for cerrado trees has not yet been determined.

Analysis of variance (ANOVA) was utilized to test for differences in total biomass, the individual components of biomass, and fire consumption among plant communities. We found that means were correlated positively with the

variance (i.e. greater means had greater variance). Therefore, data were log-transformed prior to analysis (Sokal & Rohlf 1981). However, because results of the ANOVA with log-transformed data were not different from original data at a confidence level of 90%, they are presented here without the transformation. If significant differences in communities were found ( $P \leq 0.10$ ), the protected least significant difference multiple range test was applied to determine the differences among communities.

*Fire behaviour.* Ambient temperature ( $^{\circ}\text{C}$ ), relative humidity (%), wind speed ( $\text{m s}^{-1}$ ), wind direction, and cloud cover were measured at the time of ignition. Fires were ignited as perimeter or circle fires except for the campo limpo site which was ignited with a backfire pattern (against the wind), due to high wind speeds at the time of ignition.

Observations of flame characteristics and fire behaviour were recorded at 3–10 random locations during each fire. Measurements included flame length, flame height, flame depth and flame angle (Alexander 1982). In addition, the rate of spread ( $\text{m min}^{-2}$ ), and residence time(s) were recorded (Alexander 1982, Rothermel & Deeming 1980). With these data, fireline intensity ( $\text{kW m}^{-1}$ ), reaction intensity ( $\text{kW m}^{-2}$ ), and heat per unit area ( $\text{kJ m}^{-2}$ ) were calculated according to formulas reported in Alexander (1982) and Rothermel & Deeming (1980).

*Moisture content.* At each site, at the time of ignition, moisture contents of graminoids, litter, herbaceous dicots, wood debris and soils were determined on a dry weight basis. A few minutes prior to ignition, five samples of each component were placed in air-tight soil containers and weighed in the field to determine fresh weight. In the laboratory, they were dried at  $100^{\circ}\text{C}$  for 24 h and then reweighed.

#### *Belowground biomass*

Root biomass was quantified by a combination of monolith and auger methods (Böhn 1979). Five monoliths  $50\text{ cm} \times 50\text{ cm}$  in area were sampled in each community type. The first sample was randomly selected within the stand and the others were systematically selected along a transect *c.* 20 m distant from each other. Prior to excavation, all aboveground vegetation was cut and removed and a trench was dug immediately adjacent to the area to be sampled. Roots and soil within the monolith were excavated and separated into layers (0–10, 10–20, 20–30, 30–50 and 50–100 cm). From the 100 to 200-cm depth a 15-cm diameter core was extracted with an augur and was completely sampled to determined root mass of this layer.

All materials (soil and roots) were sieved in the field. Roots were taken to the laboratory, and dried at  $60^{\circ}\text{C}$  for 48 h and weighed. Later, roots were separated into five classes according to diameter:  $\leq 5$ , 6–10, 11–20, 21–30 mm, and ‘tubers’. The tuber category includes all other belowground structures found in the cerrado, such as tubercle roots, xylopodia, lignotubers and rhizomes. A non-parametric Kruskal-Wallis test was applied to test for differences

among root biomass of communities ( $P < 0.10$ ). If significant, a Mann-Whitney U-test was applied to determine where differences among the communities existed (Sokal & Rohlf 1981).

## RESULTS

### *Pre-fire aboveground biomass*

Along the gradient from campo limpo to cerrado denso, TAGB ranged from 5.5 to 24.9 Mg ha<sup>-1</sup> (Table 1). The TAGB was significantly different between the campo limpo, campo sujo, and the woodland communities (cerrado aberto and cerrado denso). Total graminoid biomass (live and dry grasses combined) was significantly greater in the campo limpo and campo sujo than in the cerrado aberto and cerrado denso. Aboveground biomass of graminoids in campo limpo accounted for 72% of the TAGB, while in campo sujo, it accounted for 45%. In contrast, graminoids accounted for 8 and 7% of the TAGB in cerrado aberto and cerrado denso communities, respectively. Cerrado aberto and cerrado denso had significantly greater litter biomass than campo limpo and campo sujo. Biomass of small dicots, palms and bromeliads was significantly higher for cerrado aberto than for other communities (Table 1). Total dead wood debris comprised 7% of TAGB of cerrado aberto and cerrado denso and the distribution of the mass among size classes was similar in these two communities.

Among the three communities with a shrub (arvoreta) component, density was significantly higher in cerrado aberto (1347 ha<sup>-1</sup>) than campo sujo and cerrado denso (650 and 844 ha<sup>-1</sup>, respectively; Table 2a). Average basal area and height of shrubs was greatest in cerrado aberto. This was reflected in its significantly higher shrub biomass compared to other communities (Table 1).

The tree component was the most apparent structural difference among the communities (Table 2b). Tree density ranged from 0 and 28 ha<sup>-1</sup> in the campo limpo and campo sujo communities to >1000 ha<sup>-1</sup> in the cerrado denso community. Mean and maximum tree height increased along this vegetation gradient. In addition, both the mean tree size (basal area) and the total basal area of the community significantly increased along the gradient from grasslands to cerrado denso. Tree biomass was significantly higher for cerrado denso than for cerrado aberto and campo sujo (Table 1). Trees comprised 1% of the TAGB in campo limpo and campo sujo, but 27 and 52% in cerrado aberto and denso, respectively.

The fuel load is defined as the portion of aboveground biomass that is susceptible to fire consumption (e.g., biomass of downed wood, litter, herbaceous materials and shrub leaves; Kauffman *et al.* 1994). In campo limpo this was equivalent to the TAGB. The fuel load significantly increased from campo limpo to cerrado aberto, but decreased in the tree-dominated cerrado denso (Table 1).

Table 1. Total aboveground biomass ( $\text{Mg ha}^{-1}$ ) before, after fire, and the combustion factor (%) along a vegetation gradient in Cerrado near Brasilia, DF, Brazil (August–October 1993). Numbers are means  $\pm$  SE.

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												
litter	$0.6 \pm 0.1^a$	0.0	$100 \pm 0$	$1.9 \pm 0.3^b$	0.0	$100 \pm 0$	$3.8 \pm 0.3^c$	$0.0 \pm 0.0$	$100 \pm 0$	$3.3 \pm 0.2^c$	$0.0 \pm 0.0$	$100 \pm 0$
dry graminoids	$2.0 \pm 0.1^a$	0.0	$100 \pm 0$	$3.4 \pm 0.3^b$	0.0	$100 \pm 0$	$1.7 \pm 0.2^{ac}$	0.0	$100 \pm 0$	$1.4 \pm 0.1^c$	$0.0 \pm 0.0$	$100 \pm 0$
green graminoids	$1.9 \pm 0.0^a$	$0.2 \pm 0.0^A$	$90 \pm 2^A$	$7.8 \pm 0.1^b$	$0.1 \pm 0.0^B$	$90 \pm 4^A$	$0.3 \pm 0.0^c$	$0.0 \pm 0.0^B$	$95 \pm 1^A$	$0.3 \pm 0.0^c$	$0.0 \pm 0.0^B$	$91 \pm 2^A$
total graminoids	$4.0 \pm 0.3^a$	$0.2 \pm 0.0^A$	$96 \pm 1^A$	$4.2 \pm 0.4^a$	$0.1 \pm 0.0^B$	$99 \pm 0^B$	$2.0 \pm 0.2^b$	$0.0 \pm 0.0^B$	$99 \pm 0^B$	$1.7 \pm 0.1^b$	$0.0 \pm 0.0^B$	$98 \pm 0^B$
dicots, palms and bromeliads	$1.0 \pm 0.1^a$	$0.3 \pm 0.2^A$	$96 \pm 1^A$	$1.4 \pm 0.2^a$	$0.1 \pm 0.0^A$	$89 \pm 3^A$	$4.5 \pm 1.3^b$	$0.3 \pm 0.1^B$	$90 \pm 4^A$	$2.0 \pm 0.2^a$	$0.3 \pm 0.1^A$	$90 \pm 3^A$
Wood debris												
0–0.64 cm	–	–	–	–	–	–	$0.3 \pm 0.1$	$0.0 \pm 0.0$	$89 \pm 3^A$	$0.3 \pm 0.0$	$0.1 \pm 0.0$	$79 \pm 4^B$
0.65–2.54 cm	–	–	–	–	–	–	$0.6 \pm 0.1$	$0.2 \pm 0.0$	$62 \pm 8^B$	$0.6 \pm 0.1$	$0.2 \pm 0.0$	$53 \pm 8^B$
>2.54 cm	–	–	–	–	–	–	$0.8 \pm 0.1$	$0.4 \pm 0.1$	$42 \pm 10$	$1.0 \pm 0.2$	$0.5 \pm 0.2$	$39 \pm 10$
total	–	–	–	–	–	–	$1.7 \pm 0.2$	$0.6 \pm 0.1$	$67 \pm 6$	$1.9 \pm 0.2$	$0.8 \pm 0.2$	$55 \pm 6$
Surface layer												
herb layer + woody debris	$6 \pm 0^a$	$0.4 \pm 0.2^A$	$92 \pm 5^A$	$7.5 \pm 0.5^{ab}$	$0.2 \pm 0.0^B$	$97 \pm 1^A$	$12.1 \pm 2.0^b$	$0.9 \pm 0.2^{ab}$	$92 \pm 3^B$	$8.8 \pm 0.8^a$	$1.1 \pm 0.2^B$	$87 \pm 21^A$
Shrubs												
leaf biomass	–	–	–	$0.2 \pm 0.1^a$	$0.0 \pm 0.0$	$99 \pm 2^A$	$0.7 \pm 0.1^b$	$0.1 \pm 0.0$	$89 \pm 4^B$	$0.4 \pm 0.1^c$	$0.1 \pm 0.0$	$83 \pm 6^B$
total biomass	–	–	–	$1.7 \pm 0.3^a$	$1.1 \pm 0.2^A$	$27 \pm 6^A$	$6.2 \pm 0.5^b$	$3.9 \pm 0.4^b$	$35 \pm 5^A$	$3.2 \pm 0.5^c$	$2.9 \pm 0.4^B$	$10 \pm 1^B$
Fuel load	$5.5 \pm 0^a$	$0.4 \pm 0.2^A$	$92 \pm 5$	$7.8 \pm 0.7^b$	$0.2 \pm 0.0^A$	$97 \pm 3^B$	$12.9 \pm 0.9^c$	$1.0 \pm 1.0^B$	$92 \pm 2^B$	$9.2 \pm 0.1^b$	$1.2 \pm 0.2^B$	$87 \pm 2$
Tree	–	–	–	$0.0 \pm 0.0^a$	$0.1 \pm 0.1^A$	0	$6.6 \pm 1.7^b$	$6.6 \pm 1.7^b$	0	$12.9 \pm 2.5^c$	$12.9 \pm 2.5^c$	0
Total (TAGB)												
surface layer + shrub + tree	$5.5 \pm 0.3^a$	$0.4 \pm 0.2^A$	$92 \pm 5^A$	$9.3 \pm 0.8^b$	$1.4 \pm 0.1^B$	$84 \pm 1^B$	$24.8 \pm 2.5^c$	$11.4 \pm 1.2^C$	$54 \pm 4^C$	$24.9 \pm 2.9^c$	$17.0 \pm 2.6^C$	$33 \pm 3^C$
Ash	–	$0.4 \pm 0.0^A$	–	$1.3 \pm 0.9^B$	–	–	$2.2 \pm 0.3^C$	–	–	$1.5 \pm 0.2^B$	–	–

Different lower case letters denote a significant difference ( $P \leq 0.10$ ) in biomass between communities before fire. Different upper case letters denote differences in biomass between communities after fire ( $P \leq 0.10$ ). Different underlined uppercase letters denote a significant difference in combustion factors ( $P \leq 0.10$ ) between communities. The absence of letters indicate no differences were found between communities. A dash (–) denotes that components were not found in the community.



Table 2. Shrub (a) and tree (b) density, height and basal area of three community types along a vegetation gradient in Cerrado near Brasilia, DF. Numbers are means  $\pm$  SE.

(a)			
Shrubs	Campo sujo	Cerrado aberto	Cerrado denso
Density (shrubs ha <sup>-1</sup> )	650 $\pm$ 80 <sup>a</sup>	1347 $\pm$ 110 <sup>b</sup>	844 $\pm$ 97 <sup>c</sup>
Height (m)			
mean	0.81 $\pm$ 0.34	1.05 $\pm$ 0.04	0.93 $\pm$ 0.05
range	0.13 – 1.43	0.50 – 1.94	0.55 – 1.77
Basal area per shrub (cm <sup>2</sup> per shrub)*	66.4 $\pm$ 14.4	82.6 $\pm$ 8.70	74.7 $\pm$ 19.1
Basal area/ha (m <sup>2</sup> ha <sup>-1</sup> )	4.3 $\pm$ 0.9 <sup>a</sup>	11.1 $\pm$ 1.6 <sup>b</sup>	6.0 $\pm$ 1.3 <sup>c</sup>
(b)			
Trees	Campo sujo	Cerrado aberto	Cerrado denso
Density (trees ha <sup>-1</sup> )	28 $\pm$ 28 <sup>a</sup>	1069 $\pm$ 124 <sup>b</sup>	1000 $\pm$ 109 <sup>b</sup>
Height (m)			
mean	2.5 $\pm$ 2.5 <sup>a</sup>	2.92 $\pm$ 0.11 <sup>b</sup>	3.09 $\pm$ 0.35 <sup>b</sup>
range	2.4 – 2.5	2.01 – 6.00	2.01 – 10.00
Basal area per tree (cm <sup>2</sup> per tree)*	0.0 $\pm$ 0.0 <sup>a</sup>	80.2 $\pm$ 12.5 <sup>b</sup>	145 $\pm$ 16.9 <sup>c</sup>
Basal area/ha (m <sup>2</sup> ha <sup>-1</sup> )	0.0 $\pm$ 0.0 <sup>a</sup>	8.5 $\pm$ 2.1 <sup>b</sup>	14.5 $\pm$ 2.5 <sup>c</sup>

Different lower case letters denote a significant difference ( $P \leq 0.10$ ) among communities for both tables. The absence of letters indicate that no differences were found.

\* Basal area was measured at the ground-level (0 cm) for shrubs and at 30 cm height for trees.

### Fuel conditions and fire behaviour

The campo sujo, cerrado aberto, and cerrado denso communities were burned in August, 1993 prior to the onset of the rainy season compared to the campo limpo which was burned in October, 1993 following the onset of the rainy season. Weather conditions were similar at the time of burning for all communities, except for campo limpo, which had higher wind speeds (5–6 km h<sup>-1</sup>). Ambient temperatures ranged from 27 to 32°C, and relative humidity averaged 36% (Table 3). Differences in the season in which campo limpo was burned were strongly reflected in the mean moisture content of graminoids

Table 3. Weather conditions and fuel moisture content (%) at the time of prescribed burning along a vegetation gradient of Cerrado, near Brasilia, DF, Brazil. Data for fuel moisture content are means  $\pm$  SE.

	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 <sup>-1</sup> )	5–6	–	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	53 $\pm$ 3	9 $\pm$ 1	27 $\pm$ 7	24 $\pm$ 5
dicots	114 $\pm$ 12	113 $\pm$ 8	111 $\pm$ 4	137 $\pm$ 5
woody debris	–	–	5 $\pm$ 1	6 $\pm$ 1
litter	–	–	5 $\pm$ 0	5 $\pm$ 1
soil	33 $\pm$ 1	33 $\pm$ 1	20 $\pm$ 2	18 $\pm$ 1

Table 4. Fire behaviour along a vegetation gradient in Cerrado, near Brasilia, DF, Brazil. Data are means  $\pm$  SE.

	Campo limpo	Campo sujo	Cerrado aberto	Cerrado denso
Flame length (m)	1.4 $\pm$ 0.2	2.8 $\pm$ 0.5	3.1 $\pm$ 0.4	3.4 $\pm$ 0.3
Flame height (m)	1.2 $\pm$ 0.2	2.2 $\pm$ 0.5	2.7 $\pm$ 0.3	2.9 $\pm$ 0.4
Flame depth (m)	1.1 $\pm$ 0.3	3.0 $\pm$ 2.0	3.8 $\pm$ 0.4	2.8 $\pm$ 0.3
Flame angle (degree)	53 $\pm$ 7	45 $\pm$ 0	63 $\pm$ 4	61 $\pm$ 6
Rate of spread (m min <sup>-1</sup> )	2.0 $\pm$ 1.0	no data	13.8 $\pm$ 2.4	13.8 $\pm$ 0.3
Residence time (s)	no data	no data	31.6 $\pm$ 1.8	28.5 $\pm$ 6.8
Fire line intensity (kW m <sup>-1</sup> )	557	2437	3094	3693
Reaction intensity (kW m <sup>-2</sup> )	506	812	814	1319
Heat per unit area (kJ m <sup>-2</sup> )	278	no data	224	267

which is the dominant component responsible for sustained ignition and fire spread. Graminoid moisture content was very high in campo limpo (53%), while it was about half that in the woodland communities (24–27%) and quite low in campo sujo (9%). In cerrado aberto and cerrado denso, wood debris and litter had the lowest fuel moisture of all sampled components; moisture content of these components was  $\leq$ 6% (Table 3).

The influence of differences in community structure, fuel moisture conditions at the time of burning, and patterns of ignition were likely reflected in differences observed in fire behaviour of the plant communities. Flame length ranged from 1.4 m in campo limpo to 3.4 m in cerrado denso. Rate of fire spread was much slower in the campo limpo with comparatively moist fuels and with a backing fire spreading against the wind contrasted to that of the cerrado aberto and denso with drier fuels with a perimeter fire. In general, all measures of fire intensity increased along the gradient from campo limpo to cerrado denso (Table 4). For example, fireline intensity increased from 557 to 3693 kW m<sup>-1</sup> while reaction intensity increased from 506 to 1319 kW m<sup>-2</sup>.

#### *Biomass consumption by fire*

The percentages of TAGB consumed by fire (the combustion factor) were 92 and 84% for campo limpo and campo sujo, respectively. The combustion factors for cerrado aberto and denso were significantly lower at 54 and 33%, respectively. In both campo limpo and campo sujo, only minute amounts of green grass and dicots remained after burning. The combustion factor of dry graminoids and litter components for all communities was *c.* 100%. Higher consumption rates were measured for smaller compared to the larger diameter classes of wood debris. Total shrub biomass consumption (stem and leaves combined) was greatest in cerrado aberto (35%). However, shrub leaves had a combustion factor ranging from 83% in cerrado denso to 99% in campo sujo. Neither the mainstems nor the leaves of trees were consumed by fire. The consumption of the fuel load was high for all communities (87–97%), and differences were not detected among communities (Table 1). The quantity of biomass consumed by fire increased across the gradient from 5.1 Mg ha<sup>-1</sup> in campo limpo, to

13.4 Mg ha<sup>-1</sup> in cerrado aberto, but in cerrado denso, consumption declined to 8.0 Mg ha<sup>-1</sup>.

#### *Post-fire aboveground biomass*

Post-fire biomass reflected the prefire composition of the communities and their inherent susceptibility to consumption by fire. The post-fire TAGB significantly increased from campo limpo (0.4 Mg ha<sup>-1</sup>), to campo sujo (1.4 Mg ha<sup>-1</sup>), to the woodland communities (11.4 and 17.0 Mg ha<sup>-1</sup> for cerrado aberto and cerrado denso; Table 1). Shrub stems and the relatively intact trees comprised the dominant aboveground biomass components in cerrado aberto and cerrado denso after fire.

Other than trees, charred shrub stems, and ash, little else remained aboveground following fire. Ash mass was greatest in cerrado aberto and cerrado denso, and was lowest in campo limpo (Table 1).

#### *Belowground biomass*

TBGB in all communities was quite high relative to the quantity of aboveground biomass and followed a similar pattern of increasing biomass along the vegetation gradient from campo limpo to cerrado denso. TBGB in campo limpo (16.3 Mg ha<sup>-1</sup>) and campo sujo (30.1 Mg ha<sup>-1</sup>) were significantly different from cerrado aberto (46.6 Mg ha<sup>-1</sup>) and cerrado denso (52.9 Mg ha<sup>-1</sup>; Figure 1).

Root biomass was concentrated in the upper layers of the soil horizon in all communities (Figure 1). The decrease in root abundance with increasing soil depth was most dramatic in campo limpo, the community without woody vegetation. Roots in the top 10 cm comprised *c.* 50% of the TBGB in campo limpo, campo sujo and cerrado aberto, but only 31% in cerrado denso. Root biomass and the proportion of the TBGB present in the 10–20 cm soil layer increased from campo limpo (10%) to cerrado denso (31%). In all communities >80% of the TBGB was present in the upper 30 cm of the soil profile except in cerrado denso (where 71% was found in the upper 30 cm of soil). Roots present at the 30–50 cm soil depth comprised 5 to 12% of the TBGB. At depths of 50–100 cm, roots comprised 5 to 13% of the total pool. Only 3 to 4% of the TBGB occurred at a depth of 100–200 cm except in campo limpo.

Of all size classes, fine roots ≤5 mm in diameter comprised the greatest proportion of total root biomass in all communities (Figure 2). While the biomass of fine roots increased along the Cerrado vegetation gradient from campo limpo to cerrado denso, their relative contribution decreased. The relative abundance of fine roots in campo limpo, campo sujo, cerrado aberto and cerrado denso was 56, 46, 40 and 29%, respectively. Coarse root biomass (diameter classes ≥ 6 mm) increased by over five-fold along the vegetation gradient: 7.1 Mg ha<sup>-1</sup> (comprising 44% of the TBGB) in campo limpo; 16.3 Mg ha<sup>-1</sup> (54% of the TBGB) in campo sujo; 28.0 Mg ha<sup>-1</sup> (60% of the TBGB) in cerrado aberto; and 37.5 Mg ha<sup>-1</sup> (71% of the TBGB) in cerrado denso (Figure 2).

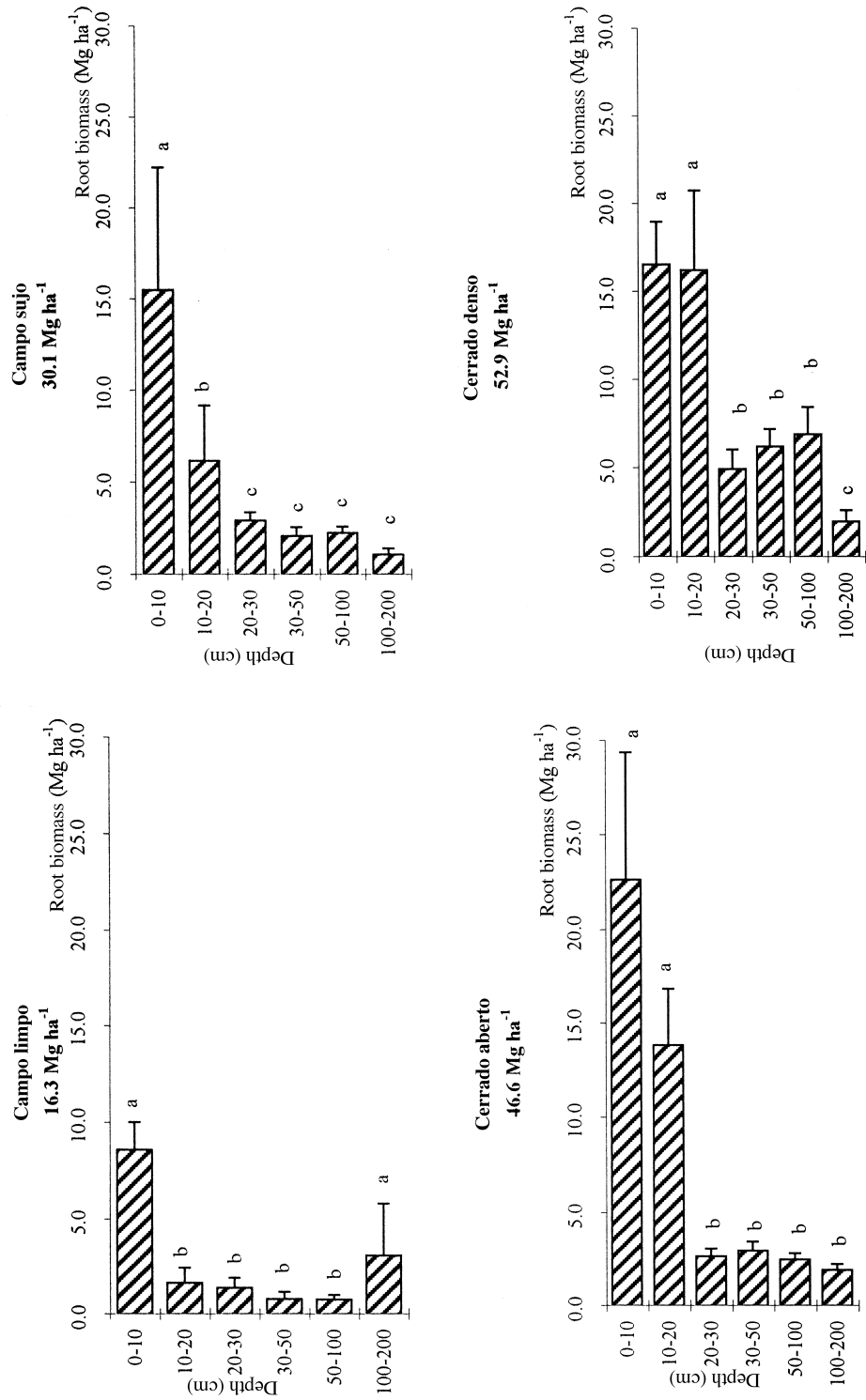


Figure 1. Root biomass distribution by depth along a Cerrado vegetation gradient near Brasilia, Brazil. Different letters refer to significant differences in biomass by depth within each community ( $P < 0.10$ ).

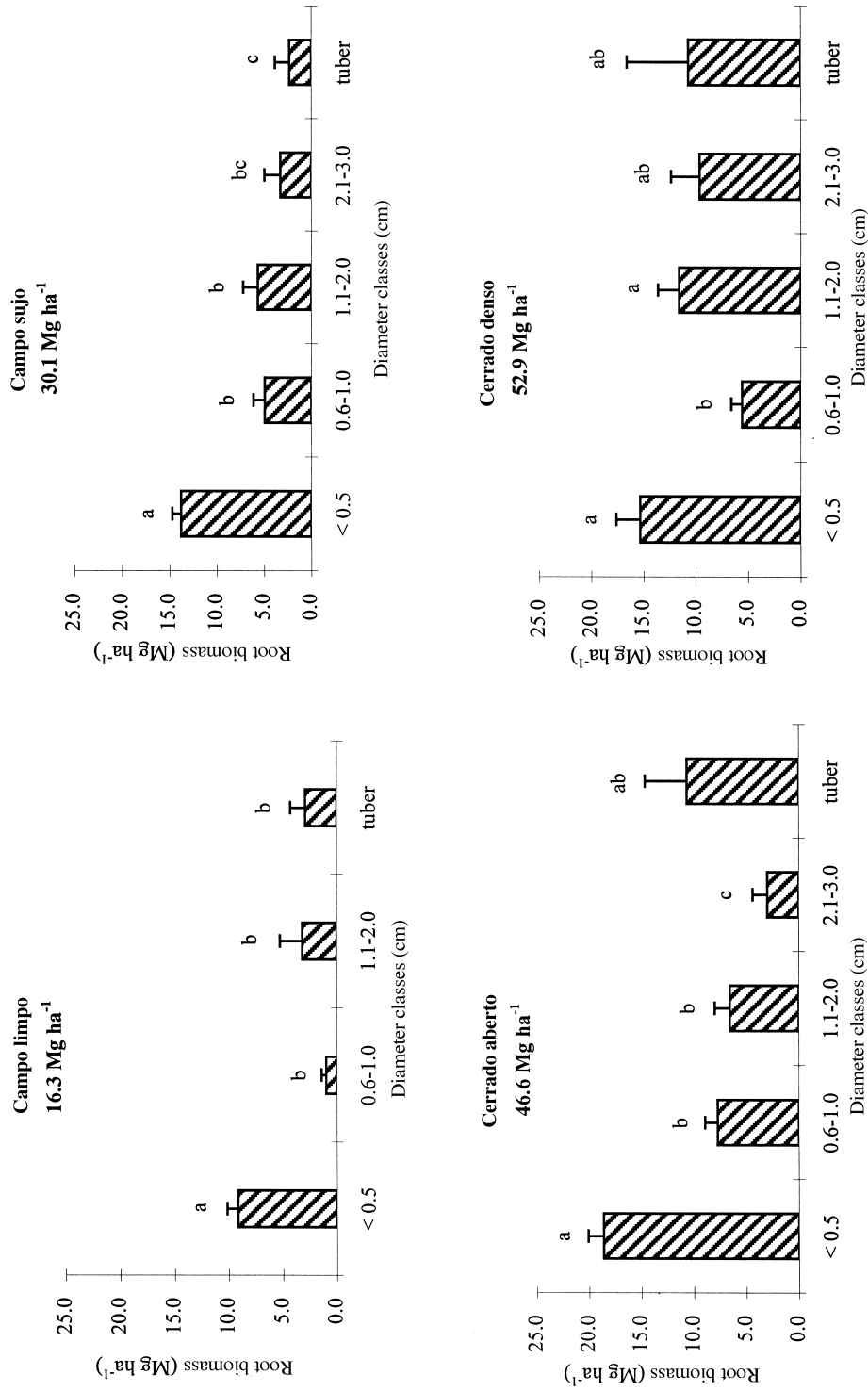


Figure 2. Belowground biomass partitioned by diameter along a Cerrado vegetation gradient, near Brasília, Brazil. In campo limpo, roots with a diameter between 2.1–3.0 cm were absent. Different letters refer to a significant differences in biomass between diameter and tuber classes within each community ( $P \leq 0.10$ ).

Tubers were present in all communities ranging from 9% of the TBGB in campo sujo to 23% in cerrado aberto.

Combining aboveground biomass data from the same sites (Table 1) with the belowground data provides a clear description of increasing structure and phytomass along this vegetation gradient. Total ecosystem phytomass (live aboveground biomass and root biomass) along the Cerrado gradient was: 19.2 Mg ha<sup>-1</sup> in campo limpo, 34.1 Mg ha<sup>-1</sup> in campo sujo, 64.2 Mg ha<sup>-1</sup> in cerrado aberto and 73.3 Mg ha<sup>-1</sup> in cerrado denso. Root:shoot ratios were higher in the grass dominated communities compared to the woodlands (Table 1). The root:shoot ratio ranged from 7.7 in campo sujo to 2.6 in cerrado aberto. Total ecosystem biomass (aboveground live and dead biomass + TBGB) ranged from 21.9 Mg ha<sup>-1</sup> in campo limpo to 77.9 Mg ha<sup>-1</sup> in cerrado denso. Belowground plant tissues comprised 65–76% of this total ecosystem biomass. In terms of the total ecosystem biomass, fires consumed *c.* 23% of that in campo limpo, 20% in campo sujo, 19% in cerrado aberto, and 10% in cerrado denso.

## DISCUSSION

### *Pre-fire aboveground biomass*

The TAGB for cerrado denso (24.9 Mg ha<sup>-1</sup>) was low compared to other common Brazilian tropical ecosystems (i.e. dry and evergreen forests) For example, Kauffman *et al.* (1993) reported that the mean TAGB of Caatinga, a Brazilian tropical dry forest, was 74 Mg ha<sup>-1</sup>. The TAGB of evergreen forests in the Amazon states of Para and Rondonia ranged from 290 to 435 Mg ha<sup>-1</sup> (Kauffman *et al.* 1995). The TAGB of the cerrado denso community in this study was <9% of the tropical evergreen forests.

The Brazilian Cerrado is not a uniform savanna ecosystem but is comprised of a mosaic of vegetation communities, each with a unique composition and structure (Eiten 1972). This is exemplified by the five-fold increase in TAGB along the gradient from campo limpo to cerrado denso. Along a similar vegetation gradient at the IBGE Ecological Reserve, Kauffman *et al.* (1994) reported a fuel load of 7.1 Mg ha<sup>-1</sup> for campo limpo, 7.3 Mg ha<sup>-1</sup> for campo sujo, 8.6 Mg ha<sup>-1</sup> for campo cerrado, and 10.0 Mg ha<sup>-1</sup> for cerrado *sensu stricto* (trees were not measured in this study). Our measurements of the biomass of campo sujo are similar, while those of campo limpo are lower (Table 1). In this study, the fuel load of cerrado aberto and cerrado denso was slightly higher than the fuel loads of campo cerrado and cerrado *sensu stricto* reported by Kauffman *et al.* (1994). These differences exemplify both annual and site variability for communities of this ecosystem. Given the large area covered by the Brazilian Cerrado (1.8 million km<sup>2</sup>) with great climatic and soil variability, caution should be made in using these biomass data as representative for all of the Brazilian Cerrado.

Based upon fuel wood inventories, Fearnside (1992) estimated the TAGB of Cerrado ranged from 11 to 52 Mg ha<sup>-1</sup>. The biomass of the cerrado denso and

aberto fall within the range proposed by Fearnside (1992), while the grassland types are much lower. Pivello & Coutinho (1992) found that the biomass of the surface layer of a campo cerrado community ranged from 4.9–7.7 Mg ha<sup>-1</sup> (trees and shrubs were not measured). This is similar to the surface layers of communities measured in this study.

#### *Fire behaviour*

Fire has both short and long-term influences on Cerrado ecosystem structure and function. The immediate influences on structure and function include consumption of aboveground biomass, nutrient loss, and transformation into ash (Kauffman *et al.* 1994, Pivello & Coutinho 1992). Variation in structure influence both the flammability and fire behaviour that occur within the communities. In addition, the influence of fire on vegetation composition and structure is a function of the fuel consumption and fire intensity which are influenced by 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 which were conducted within 13 d of one another. Therefore, differences in fire behaviour for these communities are probably due to differences in the fuel structure, arrangement, moisture content and the total quantity of biomass consumed.

Under low moisture conditions and when the distribution of grasses and/or grass litter is continuous, fires in grasslands potentially have the most rapid rate of spread of all natural communities (Brown & Davis 1973, Chandler *et al.* 1983). Campo sujo was burned at the end of the dry season when the graminoid component had a very low moisture content (9%). Compared to campo limpo, this likely contributed to the higher fireline intensity and rapid spread of fire; an area of 10 ha burned in less than 11 min. We predicted that given similar weather conditions at the time of burning, fire behaviour in campo limpo would have been equally or more dramatic than campo sujo. However, because campo limpo was burned after a series of successive rains, grass moisture content was much higher. In addition, it was necessary to use a backfire ignition pattern in campo limpo because of high wind speeds. These factors likely lowered flame lengths and rate of spread in this community.

#### *Belowground biomass*

The significant differences in TBGB tended to parallel the obvious aboveground differences in community structure along the Cerrado gradient. As aboveground biomass and woody dominance increased, biomass and structural heterogeneity of the TBGB also increased. In ecosystems such as tropical savannas with frequent fire-return intervals, the partitioning of a greater proportion of biomass belowground has been suggested to be an adaptation facilitating persistence in such a disturbance regime (Gill 1981). Environmental factors affecting root structure and biomass also include characteristics such as moisture dynamics, macronutrient availability, soil depth and other physical

characteristics (Richards 1986, Rizzini & Heringer 1961). Goodland & Pollard (1973) studied the relationship of soil chemistry and vegetation structure along a Cerrado vegetation gradient from campo sujo to Cerradão. They found higher soil nutrient concentrations in those community types with a greater tree density and basal area. Given the close proximity of the sampled sites in this study, differences in TBGB and the root structure and distribution between communities are likely the biotic reflections of site differences in chemical, physical and moisture conditions of the soil as well as the influences of fire (Kauffman *et al.* 1994).

This is the first study to quantify the TBGB to a 2-m depth in the Brazilian Cerrado. Compared with other tropical savannas and woodlands, the range of TBGB ( $16.3 \text{ Mg ha}^{-1}$  to  $52.9 \text{ Mg ha}^{-1}$ ) for the Cerrado was quite high. Along a vegetation gradient from grassland to woodland in the Venezuelan llanos, root biomass ranged from  $11.4$  to  $18.9 \text{ Mg ha}^{-1}$  (Sarmiento & Vera 1979). Along a gradient from grassland to woodland in Lamto savanna, Ivory Coast, Africa, herbaceous root biomass decreased from  $19.0 \text{ Mg ha}^{-1}$  to  $10.1 \text{ Mg ha}^{-1}$  while woody species root biomass increased from 0 to  $26.0 \text{ Mg ha}^{-1}$  (Menaut & Cesar 1979).

Although total root biomass in the Cerrado was higher than in other comparable savannas, root distribution by depth was similar. The root biomass of Venezuelan and Ivory Coast savannas also were concentrated in the surface soil layers (Menaut & Cesar 1979, Sarmiento & Vera 1979). In campo limpo, the significant decrease in root biomass below 10 cm reflects the distinctive root system displayed by graminoids which comprised 71% of the total aboveground biomass of this community. In campo sujo, cerrado aberto, and cerrado denso, root biomass declined in a more gradual manner with increasing soil depth; there was no significant difference in root biomass between the 0–10 and 10–20 cm soil depths for cerrado aberto and cerrado denso (Figure 1). This likely reflects the increasing dominance of shrubs and trees that exploit deeper areas of the soil profile. In cerrado denso, the greater abundance of roots in the 30 to 100 cm depth suggests a greater exploitation of deeper soil layers. Lawson *et al.* (1968) reported a similar stratification of roots in Guinea savanna with a greater quantity of large diameter roots of shrub and trees at depths of 20–30 cm overlain by the majority of grass roots in surface layers.

At the IBGE Reserva Ecológica, 1,100 plant species in 135 families have been identified (file data from the IBGE Reserva Ecológica herbarium). The great plant species diversity in the Cerrado implies an interspecific coexistence of species of variable root architectures, which facilitates efficient exploitation of water and nutrients at different depths. Nevertheless, the greatest proportion of the root biomass (62–79%) were concentrated in the top 20 cm of the soil horizon (Figure 1). This was similar to Lamto Savanna in Africa where 80% of the root biomass also occurred in surface soils (Menaut & Cesar 1979). While only a small proportion of roots (3–4%) were found at depths of 1–2m, roots



have been reported to penetrate as deep as 19 m in the Brazilian Cerrado (Rawitscher 1948). The ecological significance of these deep roots in terms of water and nutrient uptake is in need of further exploration.

Large roots, tubers and other belowground structures occurred in all communities but were found in the greatest abundance in the cerrado aberto and denso communities. They are organs of water, nutrient and energy storage that facilitate survival during the dry season (Rizzini & Heringer 1961). These belowground organs often possess dormant meristematic tissues that facilitate regeneration following fires. Vegetative regeneration from belowground tissues is far more common than sexual reproduction in most grasses, trees and shrubs of the Brazilian cerrado (Rizzini 1976). These are important adaptations for persistence in an environment where frequent surface fires may kill aerial plant organs but soil heat flux is minimal (Kauffman 1990). Miranda *et al.* (1993) found that during Cerrado fires aboveground temperature maxima of the flame front ranged from 85 to 840 °C. In contrast, soil was a very effective thermal barrier; negligible temperature increases were recorded below a 5-cm soil depth. When aboveground tissues are destroyed by fire, shoots arise from belowground meristematic tissues even prior to the onset of rain (Rizzini & Heringer 1961). Although trees in the Brazilian Cerrado are well adapted to fire, in the days following the burns it was observed that leaves in some tree canopies as high as 5 m in height died due to lethal scorch temperatures. We also observed that replacement of leaf area in trees and shrubs occurred within a month after loss even prior to the onset of the rainy season.

The four communities of the Brazilian Cerrado measured in this study had a very high root:shoot ratio compared to tropical deciduous and evergreen forest ecosystems (Table 4). In addition to adaptations of frequent surface fires, evergreen plants in the Cerrado persist in an environment with a pronounced dry season of 3–5 mo. However, tropical dry-deciduous forests also occur in environments with long dry seasons (Brown & Lugo 1992, Castellanos *et al.* 1991, Murphy & Lugo 1986), but without a history of frequent surface fires. Compared to dry forest, the root:shoot ratios in our sampled Cerrado communities were three times higher. This high root:shoot ratio may reflect plant adaptations to the occurrence of frequent surface fires which are common in the Brazilian Cerrado, but infrequent in deciduous and evergreen forests.

This study quantified the biomass, structure and fire consumption of plant communities along a common vegetation gradient from grassland to dense woodland in the Brazilian Cerrado. The quantity of mass, fuel arrangement, vegetation composition and resultant emissions are quite different in fires of the Cerrado compared to other Brazilian tropical ecosystems (Ward *et al.* 1992). Consumption of biomass in slash fires in the Caatinga, a tropical dry forest in Northeastern Brazil ranged from 57 to 70 Mg ha<sup>-1</sup> (Kauffman *et al.* 1993). In slashed primary Amazon evergreen forest, the biomass consumption in slash fires ranged from 125 to 227 Mg ha<sup>-1</sup> (Kauffman *et al.* 1995). However,

Table 5. Tree density (number ha<sup>-1</sup>), shoot biomass (Mg ha<sup>-1</sup>), root biomass (Mg ha<sup>-1</sup>), and the root : shoot ratio (r : s) for common tropical ecosystems.

Ecosystem	Tree density	Shoot	Root	r : s	Source	Notes
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 & Vera (1979)	(2)
woody savanna	100	5.3	19.0	3.6	Sarmiento & Vera (1979)	(2)
Ivory Coast (Africa)						
grass savanna	–	3.5	19.0	5.4	Menaut & Cesar (1979)	(3)
savanna woodland	800	61.3	37.1	0.6	Menaut & Cesar (1979)	(3)
Tropical rain forest						
Brazil						
Brazil	10406	264.0	35.4	0.1	Nepstad (1989)	(4)
Venezuela						
Venezuela	no data	335.0	56.0	0.17	Jordan & Uhl (1978); Stark & Spratt (1977)	(5)
Ghana						
Ghana	5300	233.0	54.0	0.2	Greenland & Kowal (1960)	(6)
Tropical dry forest						
Puerto Rico						
Puerto Rico	12000	53.2	45.0	0.84	Murphy & Lugo (1986)	(7)
Mexico						
Mexico	4700	73.6	31.0	0.42	Castellanos <i>et al.</i> (1991)	(8)

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

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

(3) Roots were investigated up to 1.00 m in depth. Data are the sum of herbaceous and woody roots that were presented separately in the manuscript

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

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

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

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

this is a comparison of fires burning natural savannas to anthropogenic fires in slashed forests. On an equivalent areal basis, the release of CO<sub>2</sub> as well as other emissions to the atmosphere would be dramatically lower in Cerrado fires than slash fires in tropical forest ecosystems. Moreover, because of well-adapted morphological and reproductive traits, Cerrado vegetation recovers rapidly after fire resulting in C uptake to pre-fire levels in 1–2 y.

The increase in belowground biomass from campo limpo to cerrado denso paralleled the increase of aboveground biomass along this vegetation gradient. In the Brazilian cerrado, a remarkable proportion of the phytomass is partitioned belowground. While TAGB of cerrado denso is much less than that of tropical dry and evergreen forests, the total belowground biomass was similar or even greater (Table 5). Because of the large belowground biomass, the Brazilian Cerrado may be a more significant global C pool than previously thought. While natural fires may not result in significant disruptions in the C balance of the Cerrado ecosystem, deforestation, slash burning and replacement by a crop monoculture may shift the functional role of trees and belowground pools from C sinks to atmospheric sources. In addition to altering the C budget

through slash burning and belowground C depletion, large-scale crop conversions would also result in great losses of plant diversity thereby diminishing the potential for ecosystem recovery or restoration.

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## LITERATURE CITED

- AB'SABER, A. N. 1983. O dominio dos cerrados: introdução ao conhecimento. *Revista do Servidor Publico* 111:41–55.
- ALEXANDER, M. E. 1982. Calculating and interpreting forest fire intensities. *Canadian Journal of Botany* 60:349–357.
- BÖHN, W. 1979. Methods of studying root systems. Springer-Verlag, New York. 188 pp.
- BROWN, A. A. & DAVIS, K. P. 1973. *Forest fire: control and use*. McGraw-Hill Company, New York. 686 pp.
- BROWN, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. *Forest Science* 17:96–102.
- BROWN, J. K. 1974. *Handbook for inventorying downed woody material*. USDA Forest Service., Ogden, UT. 25 pp.
- BROWN, J. K. & ROUSSOPOULOS, P. J. 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. *Forest Science* 14:350–356.
- BROWN, S., GILLESPIE, A. J. R. & LUGO, A. E. 1989. Biomass estimation methods for tropical forests with application to forest inventory data. *Forest Science* 35:881–902.
- BROWN, S. & LUGO, A. E. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia* 17:8–18.
- CASTELLANOS, J., MAASS, M. & KUMMEROW, J. 1991. Root biomass of a dry deciduous tropical forest in Mexico. *Plant and Soil* 131:225–228.
- CHANDLER, C., CHENEY, P., THOMAS, P., TRABAUD, L. & WILLIAMS, D. 1983. *Fire in forestry – fire behaviour and effects*. J. Wiley & Sons, New York. 450 pp.
- COUTINHO, L. M. 1976. *Contribuição ao conhecimento do papel ecologico das queimadas na floração de especies do Cerrado*. DSc Thesis, Universidade de Sao Paulo, Sao Paulo, SP. pp.
- COUTINHO, L. M. 1978. O conceito de Cerrado. *Revista Brasileira de Botânica* 1:17–23.
- DEEMING, J. E., BURGAN, R. E. & COHEN, J. D. 1977. *The national fire danger rating system*. USDA Forest Service, Ogden, UT. 63 pp.
- EITEN, G. 1972. The Cerrado vegetation of Brazil. *Botânica 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 deforestation in the Brazilian Amazon. Pp. 1–73 in Makundi, W. & Sathaye, J. (eds). *Carbon emissions and sequestration in forests: case studies from seven developing countries*. (Draft edition) U.S. Environmental Protection Agency, Climate Change Division, Washington DC and Energy and Environment Division, Lawrence Berkeley Laboratory, Berkeley, CA.
- FELFILL, J. & DA SILVA, Jr. M. C. 1993. A comparative study of Cerrado (*sensu stricto*) vegetation in Central Brazil. *Journal of Tropical Ecology* 9:277–289.
- GILL, A. M. 1981. Fire adaptive traits of vascular plants. Pp. 208–230 in Mooney, H. A., Bonnicksen, T. M., Christensen, N. L., Lotan, J. E. & Reiners, W. A. (eds). *Fire regimes and ecosystem properties*. USDA Forest Service. General Technical Report WO-26 Washington DC.

- GOODLAND, R. & POLLARD 1973. The Brazilian Cerrado vegetation: a fertility gradient. *Journal of Ecology* 61:219–224.
- GREENLAND, D. J. and KOWAL, J. M. L. 1960. Nutrient content of the moist tropical forest of Ghana. *Plant and Soil* 12:154–173.
- HARIDASAN, M. 1990. Solos do Distrito Federal. Pp. 309–330 in Pinto, M. N. (ed.). *Cerrado: Caracterização, Ocupação e Perspectivas*. Editora da Universidade de Brasília, Brasília.
- JORDAN, C. F. & UHL, C. 1978. Biomass of a 'Tierra Firme' forest of the Amazon Basin. *Oecologia Plantarum* 13:387–400.
- KAUFFMAN, J. B. 1990. Ecological relationships of vegetation and fire. Pp. 39–51 in Walstad, J. D., Radosevich, S. R. & Sandberg, D. V. (eds). *Prescribed fire in pacific northwest forests*. Oregon State University Press, Corvallis, OR.
- KAUFFMAN, J. B., CUMMINGS, D. L. & WARD, D. E. 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., CUMMINGS, D. L., WARD, D. E. & BABBITT, R. 1995. Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397–408.
- KAUFFMAN, J. B., SANFORD JR., R. L., CUMMINGS, D. L., SALCEDO, I. H. & SAMPAIO, E. V. S. B. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. *Ecology* 74:140–151.
- KLINK, C. A., MACEDO, R. H., & MUELLER, C. C. 1994. *Cerrado: processo de ocupação e implicações para a conservação e utilização sustentável de sua diversidade biológica*. WWF-Brasil report. 104 pp.
- LAWSON, G. W., JENIK, J. & ARMSTRONG-MENSAH, K. O. 1968. A study of a vegetation catena in Guinea savanna at Mole Game Reserve (Ghana). *Journal of Ecology* 56:505–522.
- MENAUT, J. C. & CESAR, J. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* 60:1197–1210.
- MIRANDA, A. C., MIRANDA, H. S., DIAS, I. D. F. O. & DIAS, B. F. S. 1993. Soil and air temperatures during prescribed Cerrado fires in Central Brazil. *Journal of Tropical Ecology* 9:313–320.
- MURPHY, P. G. & LUGO, A. E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88.
- NEPSTAD, D. C. 1989. *Forest regrowth in abandoned pastures of eastern Amazonia: limitations to tree seedling survival and growth*. Ph.D. Thesis, Yale University. 234 pp.
- PIVELLO, V. R. & COUTINHO, L. M. 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). J. Wiley & Sons, NY. 455 pp.
- 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.
- RAWITSCHER, F. 1948. The water economy of the vegetation of the campos cerrados in southern Brazil. *Journal of Ecology* 36:237–268.
- RAMOS, A. E. 1990. *Efeitos da queima sobre a vegetação lenhosa do Cerrado*. Masters Thesis, Universidade de Brasília, Brasília, DF. 142 pp.
- RICHARDS, J. H. 1986. Root form and depth distribution in several biomes. Pp. 82–97 in Carlisle, C., Berry, W. L., Kaplan, I. R. & Watterson, J. R. (eds). *Mineral exploration: biological systems and organic matter*. Prentice Hall, Englewood Cliffs, NJ.
- RIZZINI, C. T. 1976. *Tratado de Fitogeografia do Brasil*. Editora Hucitec e Editora da USP, Sao Paulo. 327 pp.
- RIZZINI, C. T. & HERINGER, E. P. 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. *Phyton* 17:105–124.
- RIZZINI, C. T. & HERINGER, E. P. 1962. Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. *Anais da Academia Brasileira de Ciências* 34:235–247.
- ROTHERMEL, R. C. & DEEMING, J. E. 1980. *Measuring and interpreting fire behavior for correlation with fire effects*. USDA-Forest Service, Ogden, UT. 4 pp.
- RUSSELL, R. S. 1977. *Plant root systems: their function and interaction with the soil*. McGraw-Hill, London. 300 pp.
- SAMBUICHI, R. H. R. 1991. *Efeitos de longo prazo do fogo periódico sobre a fitossociologia da camada lenhosa de um Cerrado em Brasília, DF*. Masters Thesis, Universidade de Brasília, Brasília, DF. 130 pp.
- SANFORD, R. L. Jr. 1989. Root systems of three adjacent, old growth Amazon forests and associated transition zones. *Journal of Tropical Forest Science* 1:268–279.
- SANTANTONIO, D., HERMANN, R. K. & OVERTON, W. S. 1977. Root biomass studies in forest ecosystem. *Pedobiologia* 17:1–31.
- SARMIENTO, G. & VERA, M. 1979. Composición, estructura, biomassa y producción de diferentes sabanas en los Llanos de Venezuela. *Boletín de la Sociedad de Venezolana de Ciencias Naturales* 136:5–41.
- SILBERBAUER, I. & EITEN, G. 1987. A hectare of Cerrado. I – General aspects of the trees and thick-stemmed shrubs. *Phyton* 27: 55–91.

- SKOLE, D. & TUCKER, C. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260:1905–1910.
- SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry* (2nd edition). W. H. Freeman and Company, New York. 859 pp.
- STARK, N. & SPRATT. 1977. Root biomass and nutrient storage in rainforest oxisols near San Carlos de Rio Negro, Venezuela. *Tropical Ecology* 18:1–9.
- VAN WAGNER, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science* 14:20–26.
- WARD, D. E., SUSOTT, R. A., KAUFFMAN, J. B., BABBITT, R. E., CUMMINGS, D. L., DIAS, B., HOLBEN, B. N., KAUFMAN, Y. J., RASMUSSEN, R. A. & SETZER, A. W. 1992. Smoke and fire characteristics for cerrado and deforestation burns in Brazil: BASE-B Experiment. *Journal of Geophysical Research* 97:14,601–14,619.