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REVIEW

Regional Variations in Biomass Distribution in Brazilian Savanna Woodland

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ABSTRACT

The Cerrado, the savanna biome in central Brazil, mostly comprised of woodland savanna, is experiencing intense and fast land use changes. To understand the changes in Cerrado carbon stocks, we present an overview of biomass distribution in different Cerrado vegetation types (*i.e.,* grasslands, shrublands and forestlands). We surveyed 26 studies including 170 Cerrado sites. The grasslands presented mean total biomass of 24 Mg/ha, with 70 percent allocated in the belowground portion. In shrublands, the mean total biomass was 58 Mg/ha being 58 percent in the belowground portion. Finally, in forestlands the mean total biomass was 98 Mg/ha with 18 percent as belowground biomass. The surveyed studies presented 12 allometric equations for biomass estimate, most involving both diameter and height. Data on wood density for Cerrado shrubs and trees are not abundant and the average value was 0.66 g/cm^3, similar to that found in the central portion of the Amazon Forest. We also examined the relationship between total precipitation and dry-season intensity with biomass variation in the Cerrado shrubland using data from tropical rainfall measurement mission (TRMM) for the period 2000–2010. Dry-season precipitation amount in cerrado areas in severe drought regions explained 29 percent of the variation in aboveground woody biomass. This finding is important in the face of the predictions of longer and more severe dry seasons in the region due to climate change.

Key words: allometric equations; belowground/aboveground ratio; carbon stocks; Cerrado; rainfall; wood density.

Tropical savannas occupy a large area between the equatorial rain forests and mid-latitude deserts and semi-deserts, where climate is marked by strong seasonality and where the summers are wet and winters dry (Cole 1986, Walker 1987). These savannas cover approximately 40 percent of the terrestrial tropical area (23 million km^2) and are found in Africa, Australia, South America, India and Southeast Asia (Cole 1986, Grace *et al.* 2006). Sheltering about one-fifth of the world population, these regions are under intense human impact (Grace *et al.* 2006, Goedert *et al.* 2008). The proper management of these systems is essential for understanding the balance of energy, water and carbon at both regional and global scales (Miranda *et al.* 1997, Grace *et al.* 2006).

Located primarily in the Brazilian Central Plateau region, the Cerrado has the greatest species richness and diversity among the world's savannas (Oliveira-Filho & Ratter 2002, Felfili & Silva Júnior 2005, Klink & Machado 2005). The Cerrado has high complexity of ecological determinants, in part due to its large geographic extent (Furley 1999) and proximity to other tropical biomes, such as the Amazon Forest, the Atlantic Forest, the Caatinga (seasonally dry forest) and the Pantanal (Brazilian wetlands) (Felfili & Silva Júnior 2005).

The Cerrado landscape is a mosaic of different vegetation types, ranging from grasslands to forestlands, corresponding to a gradient of woody cover (Eiten 1972, Castro & Kauffman 1998). Ribeiro and Walter (2008) described 11 phytophysiognomic types in three categories: forestlands (ciliar forest, gallery forest, dry forest and *cerradão*), shrublands (cerrado *sensu stricto*, park savanna, palm and *vereda*) and grasslands (*campo limpo, campo sujo* and *campo rupestre*) (see Eiten 1972 for a detailed description of the vegetation types).

The savanna woodlands are frequently burned during the dry season and are experiencing intense land use changes (Klink & Machado 2005, Sano *et al.* 2010). The analysis of carbon stocks and fluxes in these ecosystems is central for the understanding of human impacts on global carbon cycles through changes in land cover and use. Land conversion in the Cerrado biome has been rapid and intense in the last 40 years, mainly due to the introduction of extensive mechanized production of grains for exportation (Sano *et al.* 2010). Accumulated deforestation was estimated as 85,074 km^2 from 2002 to 2008 or 14,179 km^2

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annually. Thus, the total deforested area in the Cerrado is currently 975,636 km^2 or 47.84 percent of the total area of the biome (MMA/IBAMA/PNUD 2009).

In spite of the potential impacts of Cerrado deforestation on regional and global carbon budgets, studies focusing on temporal and spatial patterns of Cerrado productivity, carbon, and nutrient fluxes and stocks are not yet comprehensive, while the quantitation of carbon cycling in humid tropical forests has received far more attention (Grace *et al.* 2006). In a recent article, Ribeiro *et al.* (2011) assessed the above- and belowground biomass in a single Cerrado physiognomy and indicated the need for a thorough data review on biomass distribution in the different Cerrado vegetation types.

Such a review is vital not only for estimations of regional carbon cycling, but also provides a basis for implementing reducing emissions from deforestation and forest degradation (REDD) like strategies in the region. Although remote sensing, within the context of a potential monitoring, reporting and verification (MRV) system, can be used to understand the spatial patterns of biometric properties, such as biomass, ground-based data are still fundamental for the calibration and validation of these approaches. Furthermore, ground-based estimates of belowground biomass cannot be remotely assessed.

The primary purpose and contribution of this study was to provide a comprehensive assessment of biomass variation, above and belowground, in different Cerrado vegetation types, based on an extensive literature review and synthesis, including data on allometric equations, for forest and savanna physiognomies, and data about wood density. In addition, we examined the relationship between total precipitation and dry-season intensity with biomass variation in the Cerrado shrubland.

METHODS

We performed an extensive survey for articles and datasets related to biomass, carbon stocks, allometric equations, and wood density using peer-reviewed literature, technical reports and academic theses for the Cerrado region. Articles included in our review were accessed using the ISI Web of Knowledge, Google Scholar, personal communications and through library catalogs and institutions collections. Focusing on information derived from field-based measurements, we sorted and organized the studies according to the methodology of biomass quantitation: direct (*i.e.,* destructive) or indirect (*i.e.,* non-destructive) methods requiring different mathematical models (*e.g.,* Salati 1994, Higuchi *et al.* 2004). In addition, we analyzed the terminology and sampling criteria of the aboveground (*i.e.,* inclusion limits) and belowground (*i.e.,* root diameter and sampling depth) biomass.

Our analyses were based on information presented in the various articles. Information regarding biomass compartments (both above- and belowground) and wood density was extracted from the articles based on the classification provided by the authors, without performing standardization. This choice was made because of the variation in sampling criteria/classification of aboveground and belowground. Attempts to standardization based on different criteria resulted in the exclusion of important information and showed a trend of data concentration from few locations being not representative of biome. The details of the criteria and methodology of the different studies are presented in supporting information (Tables S1–S3).

In an effort to standardize the procedure throughout the analysis, all of the vegetation types defined by each of the authors were translated into the three major Cerrado vegetation categories (*i.e.,* grasslands, shrublands and forestlands) according to the classification system described by Ribeiro and Walter (2008). The grassland includes: *campo limpo*, a tropical grassland with no trees, are predominantly C4 grass species; and *campo sujo*, a shrub type savanna, encompassing both herbaceous vegetation and scattered small trees (28 trees/ha, on average, and mean height of 2.5 m). The shrubland includes the cerrado *sensu stricto*, with the subtypes sparse cerrado, typical cerrado and dense cerrado (*i.e.,* the woodland type savanna, 4–6 m height, woody density ranging from 628 to 1990 ind/ha and basal area from 6 to 18 m^2/ha). The forestland includes: *cerradão* (forest type savanna), with a canopy of nearly 70 percent, height of about 9 m, tree density larger than 2000/ha and basal area exceeding 20 m^2/ha; and gallery forest, predominantly arboreal vegetation along rivers, with a canopy of the 90 percent and height of about 25 m.

As most of the surveyed studies did not report data on fire history, soil type, land use and climatic variables, monthly tropical rainfall measurement mission (TRMM) (freely available at http://mirador.gsfc.nasa.gov/cgi-bin/mirador/presentNavigation.pl?tree=project&project=TRMM) precipitation data (Adler *et al.* 1999), at 30 km spatial resolution, for the 2000–2010 period, was acquired over the entire Cerrado biome, to understand possible environmental determinants driving variations in biomass. Because of soil heterogeneity at local level is high in Cerrado and most of the reviewed studies did not quantitate or describe soil type in a comparable form, we did not use soil type as an explanatory driver of biomass variation.

RESULTS AND DISCUSSION

We identified 26 studies that reported data on above- and belowground biomass from different Cerrado physiognomies, according to the classification proposed by Ribeiro and Walter (2008). These studies included 170 sites distributed in nine Brazilian states (Bahia, Federal District, Goias, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Roraima, São Paulo and Tocantins), with 43.5 percent of them located in Minas Gerais (Scolforo *et al.* 2008) (Fig. 1).

ALLOMETRIC EQUATIONS.—Allometric equations are indirect forms for estimating biomass, through the correlation with some easily measurable parameters without the need to destroy and weigh the plant material (Silveira *et al.* 2008). In dry climate environments, Brown (1997) recommends the use of diameter and height as variables for the biomass estimates. In the case of the Cerrado physiognomies, allometric equations have been developed for the cerrado *sensu stricto*, *cerradão* and gallery forest types (Table 1),

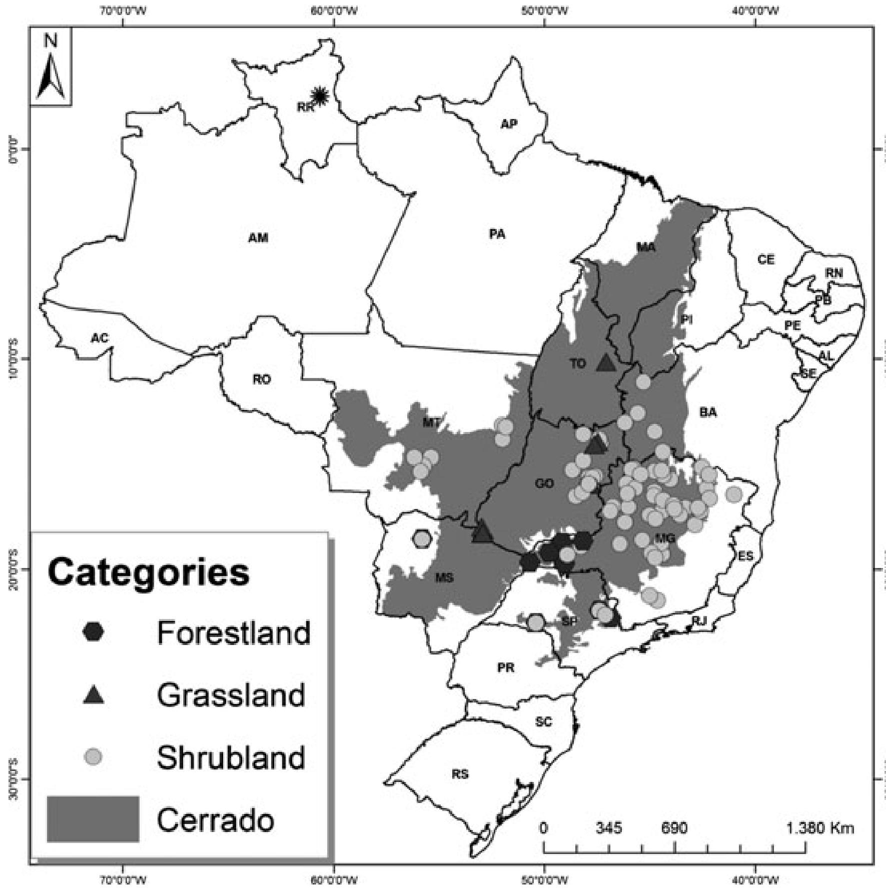

FIGURE 1. Distribution of sites where studies on above- and belowground biomass, according to different Cerrado physiognomies, were conducted. In gray, the official limits of the Cerrado biome (www.ibge.gov.br). The symbol * indicates sites from open savannas in the Brazilian Amazon.

TABLE 1. *Allometric equations used to estimate biomass and carbon stock in Cerrado. Where: B = dry biomass (kg); BD = base diameter (cm); D = diameter (cm); Dc = crown diameter (m); DBH = diameter at breast height (cm); H = height (m); AB = aerial biomass (kg/ind); dg = equivalent DBH[1]; WD = wood density (g/cm³).*

Physiognomies	Allometric equations	Parameter (kg)	Reference
Tropical Forest	$\exp\{-3.1141 + 0.9719*\ln(D^2H)\}$	Biomass	Brown *et al.* 1989,
Cerradão	$\ln(\hat{y}) = -2.8573 + 0.9556*\ln(dg^2*H)$	Total Biomass	Melo *et al.* (unpubl.) in Pinheiro 2008,
Cerradão	$\ln(\hat{y}) = -3.0363 + 0.9546*\ln(dg^2*H)$	Aerial Biomass	Melo *et al.* (unpubl.) in Pinheiro 2008,
Gallery forest	$(0.523 + 0.053*\text{perimeter})^3$	Total dry weight	Burger 1997 and Burger & Delitti 1997
Cerrado *denso* and *aberto*	$2.75*AB$	Belowground biomass	Castro & Kauffman 1998 in Felfili 2008,
Cerrado *sensu stricto*	$-0.24564 + 0.01456*BD^2*Ht$	Carbon stock	Rezende *et al.* 2006,
Cerrado *stricto sensu*	$\ln(\hat{y}) = -1.6515 + 0.7643*\ln(dg^2*H)$	Total Biomass	Melo *et al.* (unpubl.) in Pinheiro 2008,
Cerrado *stricto sensu*	$\ln(\hat{y}) = -2.6504 + 0.8713*\ln(dg^2*H)$	Aerial Biomass	Melo *et al.* (unpubl.) in Pinheiro 2008,
Cerrado	$\log(y) = 0.9967*\log(x) + 2.587$	Biomass	Eiten & Abdala (unpubl.)
Cerrado *sensu stricto*	$\ln B = \beta_0 + \beta_1 \ln DBH + \beta_7 \ln WD$	Aboveground Biomass	Ribeiro *et al.* 2011,
Campo cerrado	$28.77*(BD^2)*H$	Aerial Biomass	Delitti *et al.* 2006,
Open savannas of Roraima	$Ln(B) = 4.501 + 0.459\ln(H) + 1.589\ln(BD) + 1.025\ln(Dc)$	Live Aboveground Biomass	Barbosa & Fearnside 2005

[1]Equivalet DBH = single diameter from the basal area of trees with multiple trunks.

although the sampling schemes that were used to derive these equations did not consider the entire geographic extent of the biome, so that the spatial variation in terms of structural variables of vegetation and biomass remains highly unknown.

Studies we surveyed used 12 different allometric equations (Table 1). The number of individuals used for constraining and determining the equations ranged from 41 (Melo *et al.* unpublished data in Pinheiro 2008) to 174 (Rezende *et al.* 2006). Most of the allometric equations used diameter and height as independent variables. Only one of the equations (Ribeiro *et al.* 2011) combined wood density with diameter at breast height (dbh = 1.30 m). Ribeiro *et al.* (2011) tested five standard models combining dbh, height and wood density, and concluded that the model using dbh and woody density as explanatory variables was optimal.

WOOD DENSITY.—We found few studies that present data on wood density of Cerrado trees and shrubs (Table 2; Table S1). Most of these studies evaluated species for potential energy production (Paula 1999, 2005, Vale *et al.* 2002, 2010, Santos 2008, Thompson 2009). The studies used different methodologies and the wood density values are presented without any correction or conversion (Table S1). The values ranged from 0.52 g/cm^3 for species of *cerradão* in Federal District (Scholz *et al.* 2008) to 0.80 g/cm^3 for the cerrado species in Maranhão (Paula 2005). Overall, the mean wood density for the Cerrado species was 0.66 g/cm^3 (coefficient of variation, CV = 15%) based on data from 11 studies that sampled areas in the Federal District, Maranhão and Minas Gerais. The lowest values were found in Roraima in areas from open savannas in Amazon Forest (Barbosa & Fearnside 2004) (Table 2). For the major biogeographic regions of forest in South America, Chave *et al.* (2006) found mean values of wood density ranging from 0.60 g/cm^3 in the southwestern Amazon Forest to 0.67 g/cm^3 in its central portion (Table 2). The highest mean wood density (0.70 g/cm^3) was found for Atlantic Forest species (Table 2), while for dry forests located in central Brazil, the mean value was 0.69 g/cm^3 (Table 2).

Based on the literature data (Paula *et al.* 1998, Vale *et al.* 2002, Barbosa & Fearnside 2004, Bucci *et al.* 2004, Ribeiro *et al.* 2011), we calculated the mean wood density for 26 cerrado species with wider distribution (Ratter *et al.* 2003). *Astronium fraxinifolium* Schott ex Spreng., *Dimorphandra mollis* Benth., *Hancornia speciosa* Gomes, *Handroanthus ochraceus* (Cham.) Mattos, *Himatanthus obovatus* (Müll. Arg.) Woodson, *Hymenaea stigonocarpa* Mart. ex Hayne, *Lafoensia pacari* A. St.-Hil., *Pouteria ramiflora* (Mart.) Radlk., *Salvertia convallariodora* A. St.-Hil., and *Vatairea macrocarpa* (Benth.) Ducke can be considered heavy wood, with wood density ≥0.70 g/cm^3. *Bowdichia virgilioides* Kunth, *Byrsonima coccolobifolia* Kunth, *B. crassa* Nied., *B. verbascifolia* (L.) DC., *Caryocar brasiliense* Cambess., *Connarus suberosus* Planch., *Curatella americana* L., *Eriotheca gracilipes* (K. Schum.) A. Robyns, *Erythroxylum suberosum* A. St.-Hil., *Kielmeyera coriacea* Mart. & Zucc., *Ouratea hexasperma* (A. St.-Hil.) Baill., *Plathymenia reticulata* Benth., *Qualea grandiflora* Mart., *Q. multiflora* Mart., *Q. parviflora* Mart., and *Tocoyena formosa* (Cham. & Schltdl.) K. Schum. have values of wood density between 0.40 and 0.68 g/cm^3.

The mean wood density value for Cerrado was similar to that obtained for the central portion of Amazon Forest. In fact, more studies about wood density, encompassing at least the

TABLE 2. *Wood density data for Brazilian Tropical Forest and Cerrado.*

Biomes	Categories	Mean wood density (g/cm^3)	Federal states	References
Amazon Forest	Southwestern Amazon	0.60	–	(2)
	Northwestern Amazon	0.61	–	
	Eastern Amazon	0.64	–	
	Central Amazon	0.67	–	
	Dry Forest	0.69	–	
Atlantic Forest	Atlantic Forest	0.70	–	(2)
Cerrado	Forestland (*cerradão*)	0.52	Federal District	(10)
	Forestland (*cerradão*)	0.59	Minas Gerais	(3)
	Forestland (gallery forest)	0.65	Federal District	(8)
	Shrubland	0.59	Minas Gerais	(3), (7)
		0.66	Federal District	(9), (10), (11), (12), (13)
		0.78	Maranhão	(4), (5), (6)
		0.41	Roraima	(1)
	Grassland	0.39	Roraima	(1)

(1) Barbosa and Fearnside (2004); (2) Chave *et al.* (2006); (3) Oliveira *et al.* (2012); (4) Paula (1999); (5) Paula (2005); (6) Paula *et al.* (1998); (7) Ribeiro *et al.* (2011); (8) Santos (2007); (9) Santos (2008); (10) Scholz *et al.* (2008); (11) Thompson (2009); (12) Vale *et al.* (2002); (13) Vale *et al.* (2010).

species with wider distribution, are still necessary. Although wood density is an important variable for improving estimates of carbon stocks in vegetation (Chave *et al.* 2006), it was included in only one of the allometric equations used for biomass estimations in Cerrado. A better understanding of how wood density varies and responds to environmental factors could greatly contribute to reduction in uncertainties in carbon stock estimates in the Cerrado. In general, wood density varies from 0.13 to 1.4 g/cm^3 (Burger & Richter 1991).

ABOVEGROUND BIOMASS.—Aboveground biomass is comprised of several components, including living herbaceous and trees, as well as necromass (Keller *et al.* 2001). Total necromass, which includes litter and downed woody debris (Palace *et al.* 2012), was lowest in the grassland formations (Table 3), ranging from 0.16 Mg/ha in *campo limpo* (Ottmar *et al.* 2001) to 6.23 Mg/ha in *campo sujo* (Kauffman *et al.* 1994), both in the Federal District. For shrublands, the lowest value was found in a typical cerrado in Minas Gerais (0.46 Mg/ha) (Lilienfein & Wilcke 2003), while in a dense cerrado in the Federal District, Ottmar *et al.* (2001) found the highest value (16.61 Mg/ha). In the case of forestlands, only one study included this component. Delitti and Burger (2000) working in a gallery forest located in São Paulo estimated 3.24 Mg/ha of total necromass (Table 3).

The necromass compartment is particularly susceptible to fire (Miranda *et al.* 2004). In grassland formation with more open canopies and exposure to wind and solar radiation, the combustion efficiency is higher (98–75%) than that of more closed canopy formations (Miranda *et al.* 1996, Castro & Kauffman 1998), where the presence of shrubs and trees influences the local microclimate and changes the characteristics of fire (Miranda *et al.* 2004). Thus, the quantitation of this compartment is relevant, as fire significantly influences the emissions of greenhouse gases.

Total aboveground biomass also includes both living herbaceous and woody plants (Table 3). The values presented for forestlands were determined for a gallery forest sampled in São Paulo (133.4 Mg/ha) (Delitti & Burger 2000) and *cerradão* areas sampled in Mato Grosso and Rondônia (51.21 Mg/ha) (Fearnside *et al.* 2009). The total aboveground biomass in shrublands ranged from 2.03 Mg/ha (Kauffman *et al.* 1994) to 58.87 Mg/ha (Ottmar *et al.* 2001), while in grasslands in the Federal District, values ranged from 1.09 Mg/ha (Kauffman *et al.* 1994) to 15.60 Mg/ha (Ottmar *et al.* 2001). These variations could be related not only to the natural environmental heterogeneity of these Cerrado physiognomies, but also to different sampling methods. For example, Kauffman *et al.* (1994) conducted direct measurements along transects, while Ottmar *et al.* (2001) derived their values indirectly from a series of stereoscopic photographs (Table S2).

We found that some studies presented only the biomass of woody vegetation. Woody vegetation was defined according to different criteria, such as circumference at soil level, diameter at 30 cm from the soil level or dbh, and generally the limit of inclusion was ≥5 cm (Table S2). In forestlands, the aboveground biomass of woody plants ranged from 47.8 Mg/ha in a *cerradão* in Minas Gerais (Scolforo *et al.* 2008) to 118 Mg/ha in a gallery forest in São Paulo (Delitti & Burger 2000). In shrublands, the values ranged from 3.31 Mg/ha (Ottmar *et al.* 2001) to 67.65 Mg/ha (Ribeiro *et al.* 2011). The lowest value in grasslands was found in Roraima (0.036 Mg/ha) (Barbosa & Fearnside 2005) and the highest (5.17 Mg/ha) in a *campo sujo* in Goias (Ottmar *et al.* 2001). Because the phytophysiognomy *campo sujo* is characterized by herbaceous vegetation with scattered small trees it is expected to have a higher biomass.

BELOWGROUND BIOMASS.—Few of the studies we reviewed included the sampling of belowground biomass. In addition, these studies varied in methods applied, particularly regarding sampling depth and the classification of coarse and fine roots according to diameter (Table S3). Most the studies included sites on clayey soils (Latossolos in the Brazilian Soil Taxonomy), which covers approximately 49 percent of the Cerrado biome, while sandy soils cover 15 percent (Reatto *et al.* 2008).

Total belowground biomass values for forestlands, from two studies conducted in *cerradão* areas in São Paulo, were 15.43 Mg/ha (Delitti *et al.* 2001) and 20.18 Mg/ha (Pinheiro 2008) (mean 17.81 Mg/ha) (Table 3). In shrublands, the total belowground biomass values ranged from 5.66 Mg/ha (Pinheiro 2008) to 52.90 Mg/ha (Castro & Kauffman 1998). The highest

TABLE 3. *Mean values (Mg/ha) for biomass compartments of Cerrado. Coefficient of variation (%) in parentheses. Where: TN=total necromass, TAGB=total aboveground biomass, AGWB=aboveground wood biomass, CRB=coarse root biomass, FRB=fine-root biomass, TBGB=total belowground biomass.*

		Aboveground			Belowground		
	Number	TN	TAGB	AGWB	CRB	FRB	TBGB
Categories	of sites	Mg/ha					
Forestlands	10	3.24	92.31 (63.0)	79.66 (32.3)	–	–	17.81 (18.9)
Shrublands	128	5.98 (62.0)	21.19 (65.3)	24.56 (55.3)	17.65 (36.0)	16.63 (41.0)	33.54 (39.8)
	2[1]	0.70 (9.2)	9.19 (29.2)	6.60 (63.4)	–	–	–
Grasslands	25	2.52 (74.5)	7.15 (58.2)	1.23 (148.1)	10.70 (10.6)	10.25 (58.6)	16.72 (59.8)
	5[1]	0.42 (25.8)	5.19 (44.4)	0.32 (125.4)	–	–	1.09 (54.5)

[1]Sites from open savannas in the Brazilian Amazon (Barbosa & Fearnside 2005, Barbosa *et al.* 2012).

values for belowground biomass in grasslands were found in the Federal District and ranged from 15.9 Mg/ha (Oliveira 1999) to 30.1 Mg/ha (Castro & Kauffman 1998) both in *campo sujo*. The lowest values were found in Roraima in areas from open savannas in the Amazon Forest (Barbosa *et al.* 2012) (Table 3). In all cases, a distinction was made based on sample depth or on the diameter used for calculating the biomass stock per unit area.

Root sampling and classification is difficult and labor intensive. Most of the studies only sampled soil surface layers (up to 30 cm depth). According to Castro and Kauffman (1998), approximately 70 percent of total belowground biomass of a cerrado *sensu stricto* vegetation occurred in the topsoil layer (until 30 cm). Fewer root sampling points were conducted in deeper soil layers (Table S3), which increase the uncertainty in the estimates of carbon stocks in the Cerrado ecosystems, characterized by deep root systems (Abdala *et al.* 1998, Oliveira 1999, Rodin 2004).

RATIO OF BELOWGROUND TO ABOVEGROUND BIOMASS.—Table 4A only includes data from sites where both above- and belowground biomass were measured eliminating the effects of spatial variation, while Table 4B presents all the compiled data for aboveground and belowground biomass. The ratio of belowground to aboveground biomass decreases from grasslands to forestlands (Tables 4A and B). In grasslands, belowground biomass values showed wide variation (CV = 78.5%, Table 4A), most likely related to: (1) differences in sampling methods; and (2) variations in local abiotic factors. The data presented by Fidelis *et al.* (2013) were collected in wet grasslands, areas with high water availability in the upper soil layers, while Castro and Kauffman (1998) sampled *campo sujo* and *campo limpo* areas that were not associated with wet soils. Furthermore, the authors of the two studies reported the importance of fire in grasslands. Thus, the availability of water in the surface layer of the soil is an important factor influencing the investment in root systems and changing fire characteristics and its effect on the vegetation.

TABLE 4A. *Aboveground (Shoot) and belowground (Root) biomass for three categories of Cerrado by studies that include both estimates (above- and belowground biomass in same site).*

Categories	S (Mg/ha)	R (Mg/ha)	Depth sample of roots (cm)	Roots diameter (mm)	Diameter used in root calculation	R:S	References
Grasslands	3.9	30.1	200	≤5, 6–10, 11–20, 21–30 and tubers	Total	7.72	(3)
	2.9	16.3	200	≤5, 6–10, 11–20, 21–30 and tubers	Total	5.62	(3)
	5.1	6.16	20	Roots and belowground organs	Total	1.21	(6)
	5.58	5.74	20	Roots and belowground organs	Total	1.03	(6)
Mean (CV%)	4.37 (27.7)	14.58 (78.5)	–	–	–	3.34	
Grasslands[2]	5.65	1.14	100	<2, 2–10, >10	≥2 mm	0.20	(2)
	6.5	0.47	100	<2, 2–10, >10	≥2 mm	0.07	(2)
	8.1	1.65	100	<2, 2–10, >10	≥2 mm	0.20	(2)
Mean (CV%)	6.75 (18.4)	1.09 (54.5)	–	–	–	0.16	
Shrublands[1]	–	–	No limit for depth	≥10	≥10	0.73[3]	(5)
	19.55	30	200	<2, >2	Total	1.53	(7)
	26.02	31	620	<2, 2–10, >10	Total (less very fine)	1.19	(1)
	67.65	37.5	100	<10, >10	Total	0.55	(8)
	16.1	36.8	50	≤5, coarse roots estimated	Total	2.29	(4)
	17.2	39.7	50	≤5, coarse roots estimated	Total	2.31	(4)
	18.2	41.9	50	≤5, coarse roots estimated	Total	2.30	(4)
	23.8	45.5	50	≤5, coarse roots estimated	Total	1.91	(4)
	12.8	46.6	200	≤5, 6–10, 11–20, 21–30 and tubers	Total	3.64	(3)
	16.1	52.9	200	≤5, 6–10, 11–20, 21–30 and tubers	Total	3.29	(3)
Mean (CV%)	24.16 (69.6)	40.21 (18.5)	–	–	–	1.66	
Forestlands	–	–	No limit for depth	≥10	≥10	0.22[3]	(5)

[1]Woody aerial biomass.

[2]Sites from open savannas in the Brazilian Amazon.

[3]Root:shoot ratio for 102 trees from cerrado *sensu stricto* and *cerradão* in southeastern Brazil.

(1) Abdala *et al.* (1998); (2) Barbosa *et al.* (2012); (3) Castro and Kauffman (1998); (4) Castro-Neves (2007); (5) Durigan *et al.* (2012); (6) Fidelis *et al.* (2013); (7) Lilienfein and Wilcke (2003); (8) Ribeiro *et al.* (2011).

TABLE 4B. *Aboveground (Shoot) and belowground (Root) biomass for three categories of Cerrado in official limits (Studies that measured only aboveground biomass, only belowground biomass or both). Mean (coefficient of variation%).*

Categories	S (Mg/ha)	R (Mg/ha)	R:S	References
Grasslands	7.15 (58.2)	16.72 (59.8)	2.34	(3), (8), (11), (13), (15), (16), (21)
Shrublands	24.56 (55.3)[1]	33.54 (39.8)	1.37	(1), (2), (3), (4), (6), (7), (8), (9), (10), (12), (13), (14), (15), (16), (17), (18), (19), (20), (21), (22), (23), (24)
Forestlands	79.66 (32.3)[1]	17.81 (18.9)	0.22	(5), (6), (8), (10), (18), (23)

[1]Woody aerial biomass.

(1) Abdala *et al.* (1998); (2) Batmanian and Haridasan (1985); (3) Castro and Kauffman (1998); (4) Castro-Neves (2007); (5) Delitti and Burger (2000); (6) Delitti *et al.* (2001); (7) Delitti *et al.* (2006); (8) Fearnside *et al.* (2009); (9) Felfili (2008); (10) Fernandes *et al.* (2008); (11) Fidelis *et al.* (2013); (12) Guarino and Medeiros (2005); (13) Kauffman *et al.* (1994); (14) Lilienfein and Wilcke (2003); (15) Oliveira (1999); (16) Ottmar *et al.* (2001); (17) Paiva and Faria (2007); (18) Pinheiro (2008); (19) Rezende *et al.* (2006); (20) Ribeiro *et al.* (2011); (21) Rodin (2004); (22) Santos (1988); (23) Scolforo *et al.* (2008); (24) Vale and Felfili (2005).

In shrublands, on the other hand, the major variation occurs in the aboveground biomass (CV = 69.6%, Table 4A). This result was attributed to the different sampling methods adopted by the authors. Durigan *et al.* (2012) and Lilienfein and Wilcke (2003) used direct method for biomass sampling, Abdala *et al.* (1998), Castro and Kauffman (1998) and Castro-Neves (2007) used indirect method, and Ribeiro *et al.* (2011) combined the direct and indirect methods. In addition, different minimal limits for woody vegetation inclusion were adopted (Table S2). Differences in aboveground biomass could be related to the natural variation in the woody density of cerrado *sensu stricto.* This phytophysiognomy includes the subtypes sparse cerrado, typical cerrado and dense cerrado, with density values ranging from 628 to 1.990 ind/ha and basal area from 6 to 18 m^2/ha. Castro and Kauffman (1998) sampled sparse and dense cerrado, and the other authors sampled typical cerrado (Abdala *et al.* 1998, Lilienfein & Wilcke 2003, Castro-Neves 2007, Ribeiro *et al.* 2011 and Durigan *et al.* 2012).

The compilation of data of all studies indicates that in grasslands, the mean total biomass was 23.9 Mg/ha (Table 4B) and the belowground biomass accounted for 70 percent of this total. The root:shoot ratio (R:S) is 2.3 (Table 4B). For shrublands, the mean total biomass was 58.1 Mg/ha, with 58 percent of this in the belowground portion, corresponding to R:S ratio of 1.4 (Table 4B). In the case of forestlands, the mean total biomass was 97.5 Mg/ha, with only 18.3 percent allocated in belowground biomass, and the R:S ratio equal to 0.2 (Table 4B).

Durigan *et al.* (2012) determined root:shoot ratio of 102 trees sampled in a gradient from open- (cerrado *sensu stricto*) to closed-canopy savanna (*cerradão*) in the same region in southeastern Brazil. For *cerradão*, the ratio found was similar to that obtained based on the studies presented in Table 4B, but lower in the case of the cerrado *sensu stricto.* The sites from open savannas in the Brazilian Amazon (Barbosa & Fearnside 2005, Barbosa *et al.* 2012) have different ecological determinants than *core* areas of the Cerrado biome reflecting in the low root:shoot ratio found by Barbosa *et al.* (2012) (Table 4A). In addition to ecological determinants and natural regional environmental heterogeneity, discrepancies in calculating the R:S ratio could occur if belowground biomass values are not corrected to a standard depth and a minimum diameter (*e.g.*, >2 mm, according the IPCC guidelines).

Mokany *et al.* (2006) presented an analysis of root:shoot ratio for different ecosystems at a global scale. In comparison to their data, the R:S ratio found for the Cerrado forestlands (Tables 4A and B) was similar to values obtained for tropical forests (0.2). In the Cerrado shrublands, the R:S ratio (Tables 4A and B) was smaller than the one indicated for shrublands vegetation category (1.8), but higher than that for savannas (0.6). In addition, Cerrado grasslands had the highest R:S average (Tables 4A and B) value reported for tropical/subtropical grasslands (1.9).

Factors such as climate, soil type, water table depth and fire history influence the composition and structure of Brazilian savanna (Felfili *et al.* 2008, Ribeiro & Walter 2008, Roitman *et al.* 2008). Local variations in these factors might contribute to differences in the R:S ratio. This heterogeneity should be also taken into account in the case of subnational (or project based) mechanisms to decrease emissions of greenhouse gases from reduced deforestation and forest degradation.

Regional variations in biomass.—Our literature survey of above- and belowground biomass indicates that there is a considerable amount of variability in the Cerrado physiognomies. However, the use of different methodologies and concentration of surveys in the Southern and Central portions of the biome (Fig. 1) limit a regional estimation of carbon stocks in the Cerrado. To overcome these limitations, additional studies are necessary for the Northeast region of the Cerrado. It is also here where the dominant remnant vegetation is under intense pressure due to the expansion of commercial crops, such as soybeans and sugarcane (Sano *et al.* 2010, Rocha *et al.* 2011).

Most of the studies were conducted in shrublands (Fig. 1) due to the high areal proportion of cerrado *sensu stricto* among the Cerrado physiognomies (Felfili & Silva Júnior 1993, Sano *et al.* 2010). This physiognomy, encompassing four subtypes (typical cerrado, dense cerrado, sparse cerrado and *cerrado rupestre*) (Ribeiro & Walter 2008), occupies an area of approximately 416,000 km^2, which represents 34 percent of the 60 percent Cerrado remaining vegetation (PROBIO 2007). Considering the structural complexity of this dominant Cerrado physiognomy, additional tools are necessary to assess the geographic distribution of these subtypes.

Pontes (2010) used seasonal contrast of EVI (enhanced vegetation index) images to differentiate three seasonal classes in the cerrado *sensu stricto* physiognomy. By using primary productivity, the group found that the areas with the highest NPP (net primary productivity) values were typically the denser cerrado types. Standardized methods, likely combining remotely sensed data with ground surveys, should be established to develop baselines and monitoring systems that are fundamental parts of payment mechanisms related to mitigation of C emissions. For the cerrado *sensu stricto,* Felfili *et al.* (2005) recommended the use of basal diameter (at 30 cm from soil surface) because the individuals in this physiognomy are short, many not even reaching 1.30 m height (the standard height for diameter measuring in forests). The carbon stock decreases with the increase in diameter classes, because there is a reduction in the number of individuals in larger diameter classes (Keller *et al.* 2001, Paiva *et al.* 2011).

In forest environments, with great variation in species composition and different geographic and environmental characteristics, it remains unclear whether the use of standardized methodologies is appropriate (Saatchi *et al.* 2007). In the case of Cerrado, the transitions to other Brazilian biomes (*i.e.,* ecotones) deserve special attention, as mixtures of species of different biomes alter the biophysical structure of these areas. The highest values of woody biomass of the cerrado vegetation (between 58 and 67 Mg/ha) were found in central and northeastern portion of Minas Gerais state (Scolforo *et al.* 2008, Ribeiro *et al.* 2011), transitional areas in the Atlantic Forest, northeastern areas of Mato Grosso do Sul (Fernandes *et al.* 2008), transitional area in the Pantanal. In addition, most of the woody species that are widely distributed in the Cerrado have dense wood and the local abundance of these species influence the estimates of woody biomass and average wood density. Fearnside (1997) showed that the wood density of Amazonian trees can significantly influence the estimation of carbon stocks and indicated that studies about wood density suggested that the scientific community prioritize a careful botanical identification and evaluation of richness, as inconsistency may affect the estimates of biomass.

SEASONALITY AND DRY-SEASON PRECIPITATION DRIVES BIOMASS VARIATION.—To investigate the potential relationship between aboveground woody biomass (AGWB) and rainfall and rainfall scarcity, we analyzed the frequency distribution of AGWB found at 116 sites along the Cerrado biome for the decade of 2000–2010 (Fig. 2). The sampled areas in Roraima—Amazon Forest

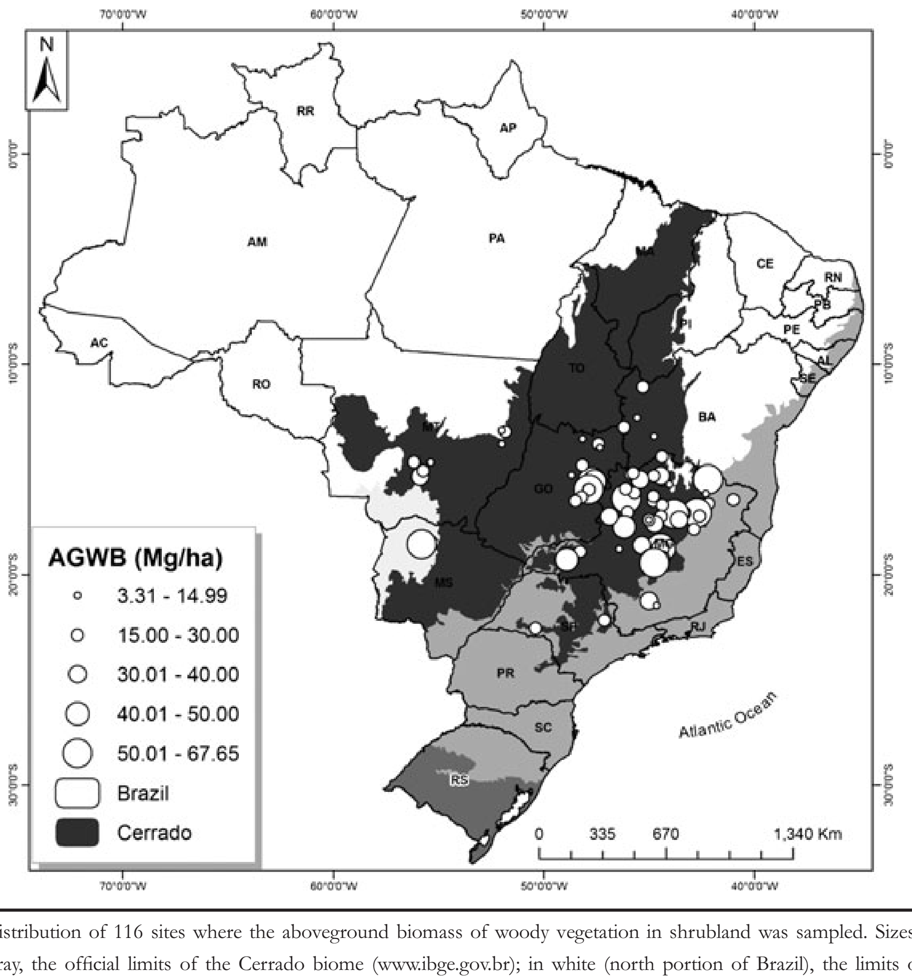

FIGURE 2. Geographic distribution of 116 sites where the aboveground biomass of woody vegetation in shrubland was sampled. Sizes of circles represent relative magnitudes. In dark gray, the official limits of the Cerrado biome (www.ibge.gov.br); in white (north portion of Brazil), the limits of the Amazon Forest; in light gray, the limits of the Caatinga (east portion) and Pantanal (west portion); east coast (medium gray), the limits of Atlantic Forest; medium gray (south portion), the Campos Sulinos limits.

biome—were excluded because different biogeographic factors are associated with their formation. The AGWB ranged from 3.31 Mg/ha to 67.65 Mg/ha and median was 21.44 Mg/ha (1st quartile = 15.15 Mg/ha and 3rd quartile = 29.31 Mg/ha). Thus, this range of biomass was used to define 'typical cerrado' areas. Regarding the geographic distribution of AGWB, the data show that, in general, the highest values are located in Minas Gerais state in transition areas with Atlantic Forest (Fig. 2).

The total precipitation in the period (2000–2010) ranged from 943 mm to 1802 mm, with median of 1339 mm (1st quartile = 1206 mm and 3rd quartile = 1380 mm) and mean value of 1314 mm (CV = 13.6%). Of the total, 82 percent of sites had MAP (mean annual precipitation) between 1100 mm and 1600 mm. Dry months were considered as those with average rainfall ≤30 mm (Eiten 1972). Dry-season length in the sites ranged from 2 to 6 mo.

Based on the biomass and precipitation data, we selected 49 sites classified as typical cerrado and with MAP between 1100 mm and 1600 mm. Mean annual precipitation (2000–2010 period) in these areas explained 15 percent (P = 0.004) of the biomass variation, with a negative relationship between precipitation and woody biomass (Fig. 3A). After 1300 mm, increased rainfall reflected in a decrease in values of AGWB.

To investigate the influence of seasonality, we separately analyzed the rainfall for rainy and dry seasons. Over 94 percent of the precipitation falls during the rainy season (MAP RAIN) and the accumulated rainfall during the rainy season explained 16 percent (P = 0.003) of the variation in AGWB (Fig. 3B). The relationship between precipitation and woody biomass was also negative. Total rainfall and accumulated rainfall during the rainy season influenced similarly the variation in biomass in typical cerrado areas (Figs. 3A and B), while the accumulated rainfall in the dry season (MAP DRY) explained 9 percent (P = 0.019) of AGWB variation (Fig. 3C). For the dry season, the relationship between precipitation and woody biomass was positive (Fig. 3C). Thus, during the dry season, increased precipitation reflected increased values for AGWB.

To evaluate the influence of drought severity on AGWB, we defined dry season based on the length, as severe (DRY SEVERE = 5–6 mo of dry season) or mild (2–4 mo of dry season). In areas where the dry season was considered mild, the accumulated rainfall was not correlated with biomass, but in areas classified as severe dry season, total dry-season precipitation was positively correlated with biomass (R^2 = 0.29, P = 0.01) (Fig. 3D). As the rainfall during the dry and wet seasons had opposite effects on the biomass, the R^2 obtained for the relationship between MAP and AGWB (R^2 = 0.15) was smaller than expected. This indicates that where drought is severe, small amounts of rain during the driest months of the year are particularly important in determining woody biomass.

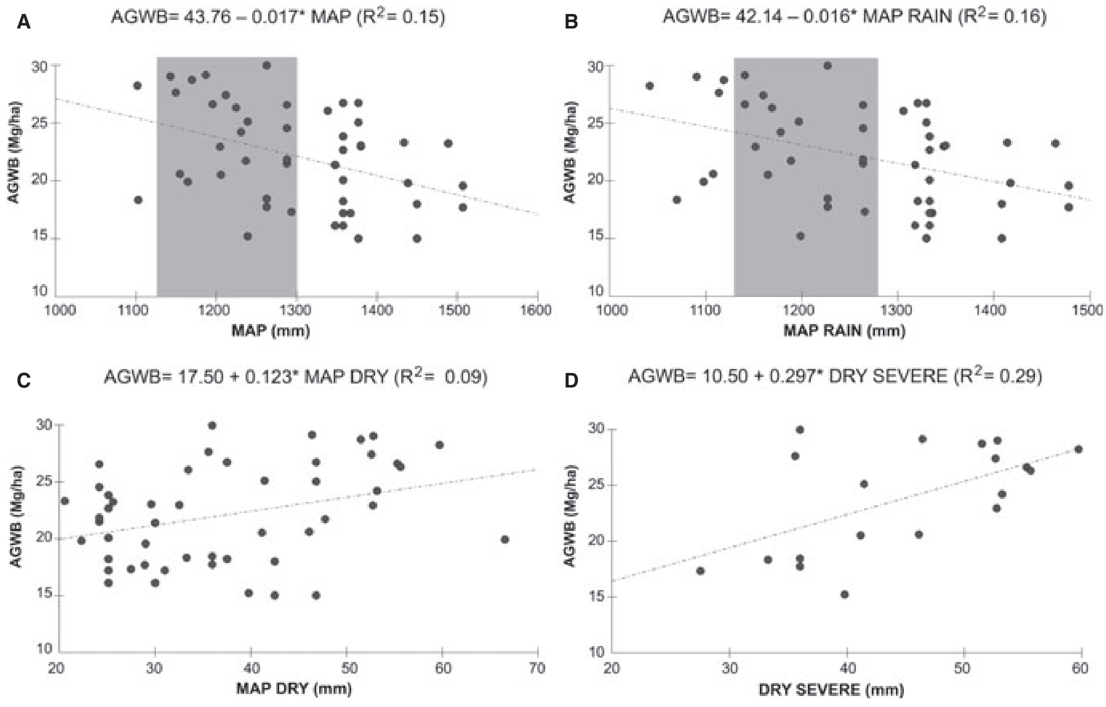

FIGURE 3. (A) Relationship between mean annual precipitation data (MAP) (2000–2010 period) and aboveground woody biomass data (AGWB) for typical cerrado. Gray zone denote highest values; (B) relationship between the accumulated mean annual precipitation during the rainy season (MAP RAIN) (2000–2010 period) and AGWB for typical cerrado. Gray zone denote highest values; (C) relationship between mean annual precipitation in dry season (MAP DRY) (2000–2010 period) and aboveground woody biomass data (AGWB) for typical cerrado; (D) relationship between precipitation in sites with severe dry season (DRY SEVERE) (2000–2010 period) and AGWB in typical cerrado.

Understanding the interactions between precipitation and disturbances is critical for predicting the effects of climate change and management practices on savanna dynamics (Liedloff & Cook 2011, Staver *et al.* 2011). According to Staver *et al.* (2011), under intermediate rainfall (1000–2500 mm) and moderate seasonality (<7 mo), the tree cover in South America savannas was distinctly bimodal, with tree cover in savannas below 55 percent and equal or greater than 55 percent in forests. In addition, the relationship between tree cover and rainfall tended to increase until 1000 mm. In the tree cover range defined by the authors for savannas (<55%), above 1000 mm, the increase in rainfall promoted a large dispersion of points.

Considering that the Cerrado is the largest savanna area in South America, our study contributes to the understanding of the relationship between rainfall and distribution of woody cover. We found that in the case of typical cerrado, the highest values of biomass are associated with the precipitation between 1100 mm and 1300 mm. Above this range, there was a tendency of decreasing AGWB, similar to that presented by Staver *et al.* (2011) for the savannas of South America. In the areas defined as typical cerrado with rainfall between 1300 mm and 1600 mm, local factors, such as fire frequency and soil texture influence the variation in woody biomass. We would have liked to include soil and other factors as indicators of AGWB, but because of local heterogeneity of soil, the fact that many studies did not include data on other environmental factors (soil included), and the lack of a regional soil map, we examined rainfall and biomass, and specifically rainfall during the dry season. We found that this was a good indicator for very dry areas and teases apart a very complex system that drives biomass across the Cerrado. We did not include belowground biomass in this effort due to the lack of studies.

The Cerrado is considered a humid tropical savanna, and in areas classified as typical cerrado, our results indicate that accumulated rainfall is not the main determinant of AGWB. For arid and semiarid savannas in Africa (precipitation <650 mm), Sankaran *et al.* (2005) found that precipitation was the main factor limiting the maximum woody cover, but in areas where the rainfall is above 650 mm, water availability does not limit the density of woody vegetation. The maintenance of savannas in this range of precipitation is the result of disturbances such as fire and herbivory. It is important to highlight that Sankaran *et al.* (2005) evaluated few sites with precipitation above 1000 mm. Our results suggest that for savannas with rainfall above 1200 mm, there are more complex interactions influencing woody cover, such as the amount of rain that falls during the drier months of the year. According Staver *et al.* (2011), the frequency peak of occurrence of savannas in South America occurred in areas with 5 or 6 mo of drought. For the typical cerrado, considering a limited subset of possible explanatory variables, the amount of rainfall during the dry season was the most important factor determining biomass variation in areas with severe dry seasons.

Regional models based on different emission scenarios of future climate change indicate that precipitation in the central and southern Cerrado may decrease 20–50 percent, while in the northeastern portion of the biome this reduction can be of 50–70 percent (Marengo 2007, Marengo *et al.* 2009). Changes in the distribution of rainfall throughout the year are also anticipated (Marengo *et al.* 2010), with the models indicating an increase in the number of consecutive days without rain (20–30 d) in the north and northeast of Cerrado. In addition, in areas of Tocantins, northern of Goias, northeastern of Mato Grosso and central region of Minas Gerais, a decrease in the number of rainy days per year is predicted. On the other hand, for the central and southern Cerrado, the models indicate an increase in rainfall. Interestingly, the models indicate more severe changes in precipitation regimes in the north and northeast Cerrado portions that are poorly sampled in terms of vegetation biomass (Figs. 1 and 2). The dearth of studies in the northern portion of the Cerrado increases the uncertainty about the influence of climate change on vegetation responses. Among the sites of typical cerrado with severe drought, 89 percent are located in the central-northern portion of Minas Gerais, where the models indicated a decrease in the number of rainy days and an increase in 2 °C in temperature, factors that can significantly influence, over the long term, the woody biomass stocks.

Cerrado vegetation types are carbon sinks during the wet season and carbon sources at the end of dry season (Miranda *et al.* 1996, 1997, Potter *et al.* 2009). This carbon flux pattern is similar to patterns observed in savannas in northern Australia (Chen *et al.* 2003). In spite of the investment in root biomass and water availability in deep soil layers during the dry season, CO_2 assimilation rates are significantly reduced for most species (Franco 2005). Changes in precipitation regime can significantly alter the carbon cycle and biomass accumulation in these ecosystems.

Saatchi *et al.* (2011) estimated standing aboveground biomass for woodland savannas to be <100 Mg/ha. When calibrating their model, the authors used only source of data from Brazil, Santos *et al.* (2003), which included only two savanna sites (Mucajai in Roraima and Comodoro in Mato Grosso). Our compiled data effectively contribute to improve regional biomass estimates for Cerrado.

Biomass values we found for shrublands and forestlands formations in the Cerrado represent substantial carbon stocks. Considering ongoing deforestation in the region (Sano *et al.* 2010, Rocha *et al.* 2011), it is important to implement mechanisms and incentives for conservation of Cerrado remnants. Discussions on mechanisms to reduce emissions of greenhouse gases from deforestation and forest degradation have focused on tropical rain forests and little attention has been paid to the potential of REDD in Cerrado. However, the introduction of such mechanisms in the Cerrado is a challenge because the biome consists of a mosaic of shrublands, forests and grasslands/cultivated areas that show marked seasonality and natural and anthropogenic fires. These factors might complicate the monitoring of land cover change and associated carbon stocks in the Cerrado, but should not prevent the implementation of positive incentives for conservation and restoration of Cerrado landscapes. Finally, ground-based data are crucial for calibration and validation of models to

TABLE 5. *Ecosystem carbon stocks (Mg/ha) in the savanna woodlands.*

Savanna Woodlands	Categories	Soil (0–20 cm)	Trees		R:S	References
			Stem	Roots		
Miombo	–	41.7	21.2	8.5	0.40	Ryan *et al.* 2011,
Cerrado	Forestland	53.0[1]	37.4	8.4	0.22	This study
	Shrubland	46.0[1]	11.5	15.8	1.37	
	Mean (weighted)[2]	48.4[2]	20.4[2]	13.3[2]	0.65	

[1]Data from Lardy *et al.* (2002).

[2]The weighted mean for the Cerrado considered the proportion of shrubland and forestland formations in the biome (6.1 and 3.2, respectively) according to Sano *et al.* (2010).

predict changes in savanna woodlands and for monitoring approaches based on remote sensing, such as those developed for tropical rain forests (Asner *et al.* 2005, Palace *et al.* 2008, Frolking *et al.* 2009). The understanding of biomass allocation (above and belowground) in this tropical savanna is essential to improve the estimates of energy, water and carbon balances, at regional and global scales.

COMPARISON BETWEEN THE CERRADO AND MIOMBO.—In Table 5, we compare data from our literature review for Cerrado vegetation types with the data presented for the Miombo by Ryan *et al.* (2011). The Miombo and Cerrado have a great physiognomic similarity and the comparison between the two major savanna woodlands highlights the importance of these systems as carbon reservoirs, with average carbon stocks of 71.4 and 82.1 Mg of C/ha for the Miombo and Cerrado, respectively. In both woodland savannas, the soil (0–20 cm depth) represents the main compartment of carbon, accounting for 58 percent of the total stock. These data, besides confirming the role of soils as the main reservoir of carbon in tropical savanna, also indicate that the removal of the tree cover can lead to a decline in the soil carbon stock over several years (Scurlock & Hall 1998).

Low soil fertility and seasonal water stress are related to a high investment in belowground biomass (12% and 16% of C stocks in the Miombo and Cerrado, respectively; Table 5). The belowground component has a higher importance in grasslands and shrublands than in forestlands in the Cerrado. Savanna species allocate more biomass to roots and less biomass to leaves and stem in relation to forest species because of the competition for light in forest environments (Hoffmann & Franco 2003). It is not only clearings that can significantly influence the carbon cycle at regional and global scales, but also inadequate soil management after conversion of these savannas (Grace *et al.* 2006). In the Cerrado, the main production systems are extensive livestock (mainly cattle) and highly mechanized croplands. While in the Miombo, it is the subsistence agriculture, with the use of fire that still predominates (Campbell *et al.* 2007, Bond *et al.* 2010). However, new pressures related to land scarcity and increasing demands for food and energy could represent drivers for more intense land use changes (Meyfroidt & Lambin 2011).

The data presented illustrate the importance of woodland savannas as carbon sinks particularly the belowground compartments (soil and root system). The analyses presented here can help to refine biomass maps and calibrate models for remote monitoring of vegetation and support public policies for the conservation of native vegetation and climate change mitigation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Sampling methodology of wood density data found in the literature.*

TABLE S2. *Sampling methodology of aerial vegetation data found in the literature.*

TABLE S3. *Sampling methodology of belowground vegetation data found in the literature.*

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