

Root biomass, root : shoot ratio and belowground carbon stocks in the open savannahs of Roraima, Brazilian Amazonia

Reinaldo Imbrozio Barbosa^{A,C}, Jhonson Reginaldo Silva dos Santos^B,
Mariana Souza da Cunha^B, Tania Pena Pimentel^A and Philip Martin Fearnside^{A,C}

^ANational Institute for Research in the Amazon, Department of Environmental Dynamic,
Av. André Araújo 2936, CEP 69060-000, Manaus – Amazonas, Brazil.

^BFederal University of Roraima, Post-graduate Program in Natural Resources, Campus Paricarana,
Av. Cap. Ene Garcez 2413 – Bairro Aeroporto, 69304-000 Boa Vista – Roraima, Brazil.

^CCorresponding author. Email: philip.fearnside@gmail.com

Abstract. Biomass of roots, the root : shoot ratio (ratio of below- to aboveground biomass) and carbon stocks belowground (to 100-cm depth) were estimated in different open savannah environments in the extreme north of the Brazilian Amazon. Sampling was conducted in permanent plots established in two open savannah areas in the state of Roraima. We identified four phytopedounits in the 27 plots sampled in two areas: four in dry grasslands on Argisol/Ultisol soils (DG-Arg), eight in dry grasslands on Latosol/Oxisol soils (DG-Lts), five in a mosaic of grasslands with savannah-parkland on Latosol/Oxisol soils (GP-Lts) and 10 in seasonally flooded (wet) grasslands on Hydromorphic/Entisol soils (WG-Hyd). Fine roots (<2 mm diameter) dominated the 0–100-cm vertical profile in the four phytopedounits (>92.5%). Biomass of the roots in WG-Hyd ($29.52 \pm 7.15 \text{ Mg ha}^{-1}$) was significantly higher as compared with the other phytopedounits studied, although the carbon stocks did not differ among the phytopedounits ($6.20\text{--}7.21 \text{ MgC ha}^{-1}$). The largest concentration of roots was found in the upper three 10-cm sections of the soil profile, ranging from 56.3 to 82.9% in the four environments. The root : shoot ratio based only on living biomass of roots with diameter $\geq 2 \text{ mm}$ (standard Intergovernmental Panel on Climate Change methodology) ranged from 0 for seasonally flooded grasslands to 0.07–0.20 for unflooded grasslands on clay soils. The results indicate that the root : shoot ratio (expansion factor) for belowground biomass in open savannah ecosystems in the northern Amazon are low and differ from the default values used in Brazil's reference report to the Climate Convention.

Received 10 December 2011, accepted 30 April 2012, published online 11 July 2012

Introduction

Savannah is a common type of vegetation in the tropics, including the Neotropics (Solbrig *et al.* 1996; Furley 1999). Their terrestrial coverage has been estimated to be $16\text{--}19 \times 10^6 \text{ km}^2$, depending on the ecogeographical definitions used (Scholes and Hall 1996; Asner *et al.* 2004). Most studies on the vertical and horizontal structures of these ecosystems are aimed at identifying structural patterns associated with biological diversity and aboveground biomass or carbon stocks. Root biomass and carbon are often not reported on a small scale because they demand so much time and effort to sample. However, even with the small number of studies, some reviews suggest that roots in tropical savannah and grassland ecosystems represent a major compartment for carbon accumulation (Jackson *et al.* 1996; Mokany *et al.* 2006). Estimates of these stocks are important for national inventories of greenhouse gases under the UN Framework Convention on Climate Change.

Generally, distribution, production and accumulation of roots are related to water availability in the soil (climatic seasonality),

which is a variable with strong temporal fluctuations in the more superficial soil layers in savannahs and grasslands (San José *et al.* 1982; Baruch 1994; Delitti *et al.* 2001). Other factors have been investigated in order to understand which processes regulate subterranean biomass, such as physiognomic structure (Sarmiento and Vera 1979; Castro and Kauffman 1998), nutrient availability (Kellman and Sanmugadas 1985; February and Higgins 2010), human alterations (Fiala and Herrera 1988), fire (Menaut and Cesar 1979; Castro-Neves 2007) and grazing (Pandey and Singh 1992; Milchunas and Lauenroth 1993; McNaughton *et al.* 1998). These studies make it possible to assess parameters such as root : shoot ratio (the 'expansion factor' used for inferring belowground biomass from aboveground biomass measurements) and rates of growth of root biomass under different successional paths, which are crucial to the understanding of belowground carbon allocation. However, no study has been conducted in Amazonian savannahs.

In savannahs, the thicker roots represent an important reservoir of carbon at greater depths, especially in physiognomies that are

more densely populated by trees (Abdala *et al.* 1998; Schenk and Jackson 2002a). However, these open-vegetation environments are characterised by having large grassy expanses and a low-density tree component. Most roots in these ecosystems are located in the most superficial layers of the soil and are characterised by having small diameters (<2 mm) (Knoop and Walker 1985). It is estimated that the different forms of savannahs (open and wooded) contain ~20% of all of the fine-root biomass on Earth to a depth of 30 cm (Jackson *et al.* 1997). This category of roots has a high rate of replenishment in tropical grasslands and savannahs, making it a critical component in sequestering atmospheric carbon by allowing constant accumulation of organic matter in the soil (Stanton 1988; Gill and Jackson 2000; Chen *et al.* 2004). However, the Intergovernmental Panel on Climate Change (IPCC 2006) suggests that this category of roots (<2 mm in diameter) should not be included as part of the 'belowground biomass' because it is difficult to distinguish it empirically from soil organic matter.

Savannahs, grasslands and other natural non-forest ecosystems occupy ~200 000 km² (~5%) of the Brazilian Amazonia (Santos *et al.* 2007). Although the area of these ecosystems is substantial, all existing studies on the biomass of roots in natural vegetation in the Amazonian biome in Brazil are from forest ecosystems due to the much larger area of forests (Klinge 1973; Luizão *et al.* 1992; Thompson *et al.* 1992; Nepstad *et al.* 1994; Cattanio *et al.* 2004). Estimates of the temporal dynamics and spatial distribution of roots in different phytophysionomies of Amazon savannahs are nonexistent, representing an important lacuna in our knowledge about this potential belowground carbon reservoir in the Amazon. These data are important for understanding the role of these environments in mitigating global warming (IPCC 2007).

The first Brazilian inventory of greenhouse gases, which was submitted to the Climate Convention (UN Framework Convention on Climate Change) in 2004, did not consider the roots, explaining that 'the consideration of carbon below ground (roots) is complex and was not included in this inventory' (Brazil MCT 2004, p. 146). Of course, considering the carbon stock in roots to be zero, and consequently considering the emission from this source to be zero after clearing the vegetation, represents a substantial underestimation, especially in savannahs, where the great majority of the biomass is below ground. The second Brazilian inventory used the default root:shoot ratios values presented by IPCC (2003, p. 3.109, table 3.4.3) to estimate total biomass for all grassland and savannah environments listed in Brazil MCT (2010, pp. 236–237). This was done both for the *cerrados* of central Brazil and for Amazon savannahs. The root:shoot ratio is an expansion factor used to estimate belowground biomass from aboveground biomass (IPCC 2006, p. 6.7). However, use of the IPCC default values for calculating belowground biomass in open-vegetation systems under different environmental conditions can cause undesired distortion in the final values for total biomass.

Within this context, our goal was to estimate the biomass of roots in different open savannah environments in Roraima in view of the combination of two effects (phytophysionomic structure and soil class, forming a 'phytopedounit'). The phytopedounits presented here are similar to the 'landscape system units' defined by Sombroek *et al.* (2000). A classification including both

vegetation and soil effects is important in order to prevent phytophysionomies with the same structure on different soil classes from being analysed as the same ecological unit. This strategy includes spatial variations that occur along different edaphic gradients that may affect the modelling of root biomass (Espeleta and Clark 2007).

The current study included the following questions: (i) Does the allocation of total carbon to roots differ among open savannahs on different phytopedounits? (ii) Does the vertical distribution of root biomass differ among these environments? and (iii) Does the ratio between the biomass of roots (total and ≥ 2 mm) and the aerial biomass (root:shoot) differ among the phytopedounits investigated? Our results represent an opportunity to reformulate the estimates of belowground biomass and carbon stocks in Amazonian savannahs, providing appropriate regional values for open-vegetation systems with low densities of trees and shrubs.

Materials and methods

Savannahs of Roraima

Savannahs of Roraima are part of the Rio Branco-Rupununi complex located in the triple frontier between Brazil, Venezuela and Guyana (Beard 1953; Eden 1970). Altogether, these continuous savannahs cover 68×10^3 km², the Brazilian part being $\sim 43 \times 10^3$ km² (~63%) (Barbosa *et al.* 2007; Barbosa and Campos 2011). In general, these savannahs are located on poor soils with high frequency of fire and strong climatic seasonality that directly influences the fluctuation of the watertable and the phytophysionomic structure (Miranda *et al.* 2003; Barbosa and Fearnside 2005a). The climate type of this whole region is Awi according to the Köppen classification, with average rainfall of ~ 1650 mm year⁻¹; the peak of the dry period is between December and March and the rainy period between May and August (Barbosa 1997). These savannahs have a wide variety of phytophysionomies ranging from grasslands that are totally devoid of trees to densely populated types on different soil classes (Brazil Projeto RADAMBRASIL 1975; Barbosa and Fearnside 2005b). The Venezuelan *llanos* have structure and species composition that are similar to those of the savannahs of Roraima (San José and Fariñas 1983; Medina and Silva 1990) and neither of these should be confused with the savannahs (*cerrados*) of central Brazil (Eiten 1978).

Study areas

The study was carried out in two savannah areas that have sample grids for a Research Program on Biodiversity: (i) Água Boa Experimental Station (AB) and (ii) Cauamé or 'Monte Cristo' Campus (MC) (Fig. 1). The grids are composed of walking trails in the North–South (N–S) and East–West (E–W) directions that cross the area at intervals of 500 m. All sampling was performed based on permanent plots (10 m \times 250 m) that are systematically distributed at points equidistant from the intersections of E–W and N–S trails. Each plot is an independent sampling unit that follows the contour line established beginning from the initial picket. This configuration was adopted to minimise the effects of topographic variability in each plot (Magnusson *et al.* 2005). All plots are individually classified by soil class and vegetation

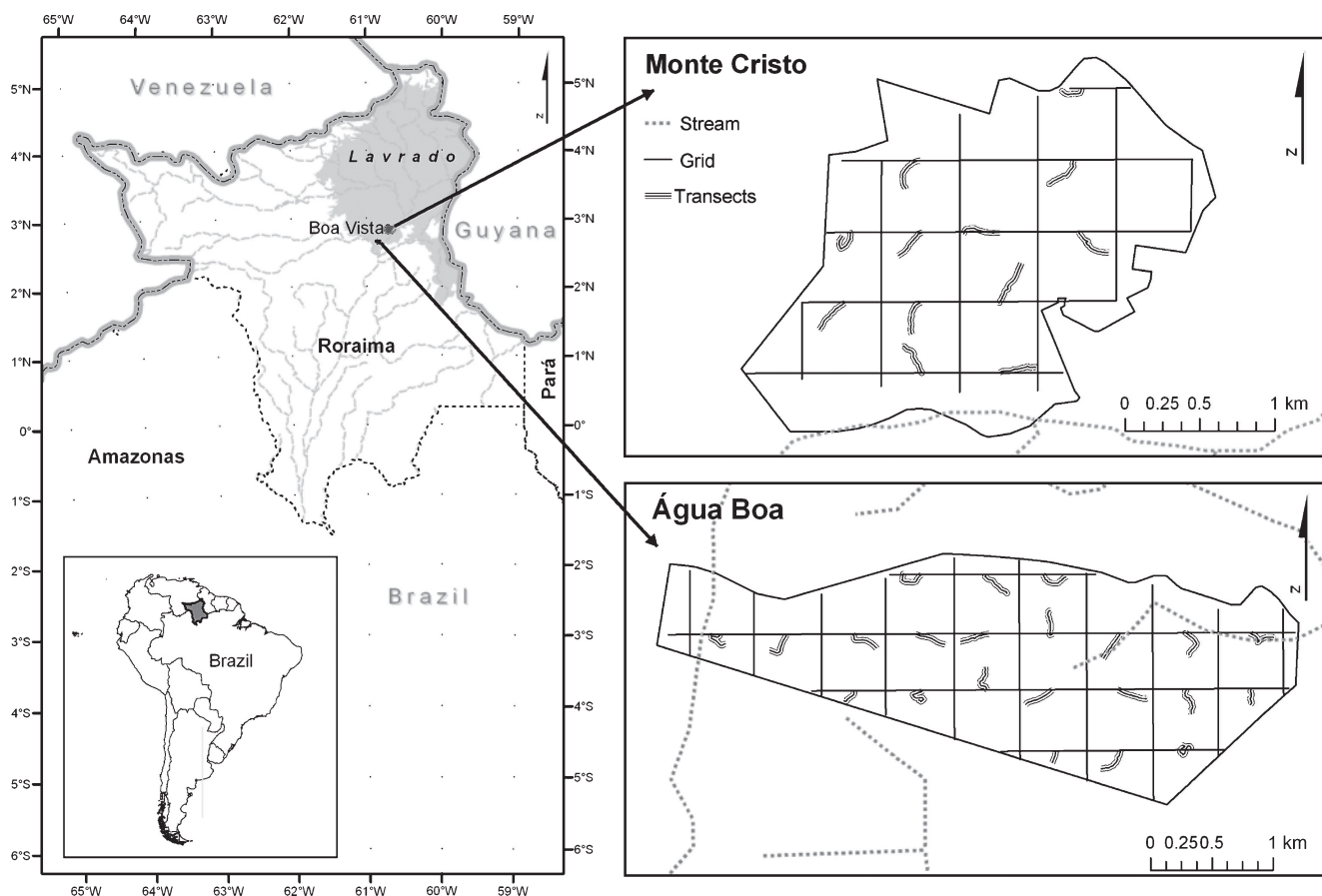


Fig. 1. Location of the two sample areas established in savannahs (*lavrado*) in Roraima, Brazil.

physionomy. The general descriptions of the sample sites are given below.

Água Boa Experimental Station (AB)

This experimental station of the Brazilian Enterprise for Agriculture and Ranching Research (EMBRAPA-Roraima) is located ~35 km south of the city of Boa Vista, on the BR-174 Highway ($2^{\circ}51'49''\text{N}$, $2^{\circ}53'6''\text{N}$ and $60^{\circ}44'14''\text{W}$, $42^{\circ}60'27''\text{W}$). The grid area is 616 ha and relief is typically flat with an average altitude of 77.7 ± 1.3 m. Seventeen of the 22 terrestrial plots in this grid were sampled. The soil classes determined by Brazil's National Soil Survey and Conservation Service indicate that most of the area has low fertility and high aluminium toxicity (Brazil SNLCS 1996).

Most of the grid is seasonally flooded grasslands with various species of Poaceae and Cyperaceae (Araújo and Barbosa 2007). In this area the soils are typically hydromorphic and of sandy texture due to an association of Gleysols with quartzarenitic Neosols (Entsols). A smaller part of the grid has two types of savannah on clay soils that are not exposed to periodic flooding (dry grasslands) and are characterised by the high density of the tree-bush component: (i) low density (<5% canopy cover), represented by grassland savannahs mixed with scrubby savannah (shrublands) and (ii) medium density (5–20%), characterised by shrublands mixed with grassland and

savannah-parkland. In this sector of the grid the soil is well drained and problems of flooding are not present.

Cauamé Campus (MC)

The Cauamé Campus, known as 'Monte Cristo', belongs to the Federal University of Roraima and is situated ~15 km north of the city of Boa Vista on the BR-174 Highway segment that leads to the border with Venezuela ($2^{\circ}38'7''\text{N}$, $2^{\circ}40'11''\text{N}$ and $60^{\circ}49'25''\text{W}$, $60^{\circ}52'28''\text{W}$). The grid has an area of 498 ha with an average altitude of 77.3 ± 4.9 m. The relief is flat to gently rolling and is derived from the Apoteri Geological Formation. This area is the most densely wooded type on clay soils. Ten of the 12 terrestrial plots in this grid were sampled. The soil classes were determined by Benedetti *et al.* (2011), indicating that this grid has soils with better drainage as compared with the Água Boa grid.

Sampling design and procedures

The sampling period for collections and field assessments was between 3 June 2009 and 27 February 2010. Samples were paired in all plots between the rainy and the dry season. We adopted this criterion in order to avoid distortions that would either under- or overestimate biomass depending on the collection period. This was necessary because there is strong seasonal variation in root production in grassland and savannah areas (Neill 1992).

Our first goal was to quantify total aboveground biomass through direct methods (for herbaceous vegetation) and indirect methods (for trees and bushes). We sampled roots using two methods: (i) direct (destructive) to understand the vertical distribution of small-diameter roots, which are generally associated with grasses and herbs, and (ii) indirect (regression) to calculate the total biomass of the root crown in the tree-bush component. Although the term 'root crown' is usually used to refer to roots located immediately below the surface of the soil under the main stems of the plants (Snowdon *et al.* 2000), we use this term to specify coarse roots at the transition point between stem and soil, including all roots ≥ 10 mm in diameter up to 1-m depth. The term 'root crown' has been used by Abdala *et al.* (1998) to refer to roots in this diameter and depth range that are located directly beneath the aerial portion of the tree, thereby distinguishing these roots from roots of the same diameter located in the open spaces between the trees. However, in the case of open savannahs in Roraima, where trees are widely spaced and root diameter distributions are dominated by small- and medium-diameter roots, the biomass of roots ≥ 10 mm in diameter is negligible in the open spaces, and a separate category for these roots would have minimal effect on the overall total.

Total aerial biomass was estimated from the sum of its two components: (i) herbaceous and (ii) tree-bush. Herbaceous biomass was defined as 'grasses' (Poaceae, Cyperaceae, seedlings, small dicots and litter) and woody individuals with diameter at the base (Db) < 2 cm, measured at 2 cm above the ground. We sampled this group by establishing four subsampling points in each permanent plot. The first subsample was established just to the right (R) of the 50-m picket, perpendicularly at a distance of 5 m from the reference line for the central trail in the permanent plot. This procedure was performed alternately using the picket at 100 m (L-left), 150 m (R) and 200 m (L).

After marking the four points we used a 1-m² metal frame to delimit the area for destructive sampling. All individuals in this group within the metal frame were cut close to the ground using metal blades. They were then weighed to obtain the wet weight corresponding to the subsample point. A composite sample of herbaceous biomass (80–150 g) was brought to the laboratory for determination of its dry weight after drying in an oven at 70–75°C until constant weight. The total herbaceous biomass in each plot was estimated by discounting the water content from the total fresh weight of each subsample and then calculating a simple mean of the four subsamples.

To estimate the total carbon corresponding to the herbaceous biomass we used the carbon content (%C), in the form of a weighted average of the different components of this group as described by Barbosa (2001). The weighted average of %C was calculated separately for each experiment station: 34.4% (MC) and 36.2% (AB).

Live tree-bush biomass was defined as the group of woody individuals composed of two vertical strata (tree and bush or shrub) as set in Miranda *et al.* (2002) and Barbosa *et al.* (2005). The area used for sampling the arboreal stratum was 10 m \times 250 m, while the shrubs were sampled in a subplot (2 m \times 250 m). The central trail of the plot was always used as the baseline for the sampling. All individuals in the tree-bush

group were identified taxonomically and inventoried by measuring biometric parameters: Db = diameter of the base of the stem measured at 2 cm above the ground; D₃₀ = diameter of the stem measured at 30 cm height; Dc = diameter of the canopy calculated as the average of the largest and smallest individual crown diameter; Ht = total height, defined as the distance from the insertion of the stem in the ground to the top of the canopy. These parameters were used to indirectly estimate the biomass of each tree-bush individual based on the regression model developed by Barbosa and Fearnside (2005b) for savannahs in Roraima. Tree-bush biomass of each plot was derived from the sum of all individual biomasses.

The carbon corresponding to the tree-bush biomass of species inventoried in the two grids was estimated from data derived from Barbosa (2001) for biomass of savannah species in Roraima, according to the weighting given in Supplementary material part A.

Total biomass of roots

Direct method (destructive)

The sampling of root biomass using the direct (destructive) method came from the same four subsampling points established for herbaceous biomass estimates. The goal of this method was to obtain mean data for each plot at five depths in the soil column: 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm and 40–50 cm. This method checks the inventory and the vertical distribution pattern of small-diameter roots present along the altitudinal gradient in the plots. In general, these roots are associated with grasses, herbs and the lateral roots of the small-diameter individuals of the tree-bush component.

Each subsample was obtained at the exact geometric centre of the metal frame used to delimit the area for destructive sampling of the herbaceous biomass. We used a soil collector measuring 0.8 m in length by 0.1 m in diameter adapted for collecting soil at depths up to 0.5 m. Each sample was placed directly in a plastic bag identified individually by depth, and was then weighed to obtain the net weight in the field. The samples were then forwarded to the laboratory for separation of the roots and for determination of air-dried weight. These weights allowed calculation of soil density (dry weight of the soil divided by its saturated volume) for each 10-cm section of the soil column.

We separated live roots manually, packing them in plastic bags identified by the plot, the subsample point and the depth in the profile. After this initial screening and separation, the residual soil was subjected to the floatation process as suggested by McKell *et al.* (1961). This method consists of adding water to the residual soil so that the lighter plant material that was not visible in the first separation would float and could be collected and added to the roots separated in the previous stage. After this process the roots were placed in a drying oven at 70–75°C until they attained constant weight.

Throughout the process all of the collected material was separated by diameter category (d) using the classes suggested by Abdala *et al.* (1998): $d < 2$ mm (very fine and fine roots) $2 \leq d < 10$ mm (medium) and $d \geq 10$ mm (coarse). After sorting, washing and drying, all categories were weighed individually to obtain the mean biomass of roots by diameter category, depth section, plot and phytodominant.

Indirect method (root crown)

This method was to estimate the biomass of the 'root crown' (as defined above) of the individual trees or bushes with $D_{30} \geq 2$ cm. In open savannah ecosystems of Roraima the tree-bush component is present at low density, and our destructive method therefore cannot provide values for the biomass of the root crown of trees and shrubs. We therefore used an indirect method, applying the linear regression of Abdala *et al.* (1998) to estimate this category. We assumed that the values derived from the regression correspond to the 'root crown' (roots ≥ 10 mm in diameter) connected to the trees and bushes with $D_{30} \geq 2$ cm up to 1-m depth.

Laboratory analyses

All of the biomass of roots collected by the direct method was separated by plot and vertical section of depth, and then ground using a knife mill. The samples were then sent to the Soil and Plant Thematic Laboratory at the National Institute for Research in the Amazon, Manaus, Amazonas, Brazil, for determination of carbon content (%C). The %C was determined using a CHN Auto-Analyzer (Vario MAX, Elementar, Germany). This equipment performs the analysis by combustion at high temperatures, followed by reduction (Nelson and Sommers 1996). In the case of %C for the root crowns of trees and shrubs we used the same values for aboveground tree-bush biomass.

Data analysis

The differences between all values obtained for the herbaceous and tree-bush components and for the total biomass in each environment were verified using the Kruskal–Wallis non-parametric test ($H_{0.05}$) (Zar 1999). In cases where the null hypothesis (equal means) was rejected, the Student–Newman–Keuls test was applied for multiple comparisons ($P < 0.05$).

All values for root biomass (total biomass and biomass by diameter category) were transformed into units of weight per unit area, for each 10-cm section of the soil profile. Using the results for the biomass of roots for each section of the 0–50-cm soil profile, we derived an estimate for the 50–100-cm section. This estimate was to combine the information from this method with the same profile (0–100 cm) adopted for calculating the root crown. For both, each result obtained from destructive subsamples (0–50 cm) was applied using an exponential model

($Y = a \times b \times e^{-X}$), with a unique value for the 50–100-cm section for each subsample (see Jackson *et al.* 1996).

Different sections up to 1-m depth were summed to determine the biomass in the vertical soil column. We also used the Kruskal–Wallis test ($H_{0.05}$) to assess biomass differences (by diameter category and total) in the soil column and the vertical distribution patterns of biomass in all environments. The total biomass per unit area for roots to 1-m depth was added to the values estimated by regression for root crowns in the tree-bush stratum.

Carbon allocation in aerial biomass and roots was calculated from the multiplication of each of these groups by the corresponding carbon fraction. For calculating the root:shoot ratio for each phytopedunit we used the values of live aboveground and belowground biomass and carbon (direct and indirect methods). We also carried out a separate analysis for roots with diameter ≥ 2 mm (direct and indirect methods). The purpose of this second analysis was to provide values for Amazon open savannahs that could be used in the national inventory, as recommended by the IPCC (2006, p. 8).

Results

Aboveground biomass and carbon

Four phytopedunits were observed in the 27 plots sampled in the two experimental grids in open savannahs in Roraima. The main tree-bush species present in dry grasslands both on Argisols (DG-Arg) and on Latosol (DG-Lts), as well as in the more densely wooded landscapes (GP-Lts), were *Curatella americana* L. (Dilleniaceae), *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae) and *B. coccolobifolia* Kunth (Malpighiaceae). In wet grasslands (WG-Hyd) woody individuals were not found with $D_{30} \geq 2$ cm.

Herbaceous and tree-bush biomasses differ significantly among environments (Table 1). The total herbaceous biomass of WG-Hyd ($9.01 \pm 2.86 \text{ Mg ha}^{-1}$) was the largest value among all of the phytopedunits, although it only differed from the DG-Arg environment. No significant difference was detected between the largest total biomass (WG-Hyd) and the other phytopedunits due to a greater presence of the tree-bush component in the dry grasslands and in the mosaic of grasslands with parkland savannahs.

The WG-Hyd phytopedunit had the largest carbon stock in the herbaceous component ($3.26 \pm 1.04 \text{ MgC ha}^{-1}$), but GP-Lts

Table 1. Aerial biomass distribution by group in different phytopedunits in two grids of open savannahs in Roraima, Brazil (mean \pm s.d.)

Values in parentheses represent the plot's live component (Mg ha^{-1}) with the litter (dead biomass) already discounted. Different lowercase letters indicate distinct significance among values in each column (Student–Newman–Keuls test; $P < 0.05$). AB = Água Boa; DG-Arg = dry grasslands on Argisols; DG-Lts = dry grasslands on Latosols; GP-Lts = mosaic of grasslands with savannah-parkland on Latosols; MC = Cauamé/Monte Cristo; WG-Hyd = wet grasslands on Hydromorphic soils

Phytopedunit	Number of plots (<i>n</i>)		Herbaceous	Tree-bush	Total
	AB	MC			
DG-Arg	0	4	$5.25 \pm 0.36a$ (4.59)	$1.06 \pm 0.68bc$	$6.31 \pm 0.88a$ (5.65)
DG-Lts	5	3	$6.74 \pm 1.91ab$ (5.89)	$0.60 \pm 1.08b$	$7.34 \pm 1.96a$ (6.50)
GP-Lts	2	3	$6.10 \pm 2.78ab$ (5.34)	$2.76 \pm 1.59c$	$8.87 \pm 2.43a$ (8.10)
WG-Hyd	10	0	$9.01 \pm 2.86b$ (7.65)	0.00a	$9.01 \pm 2.86a$ (7.65)

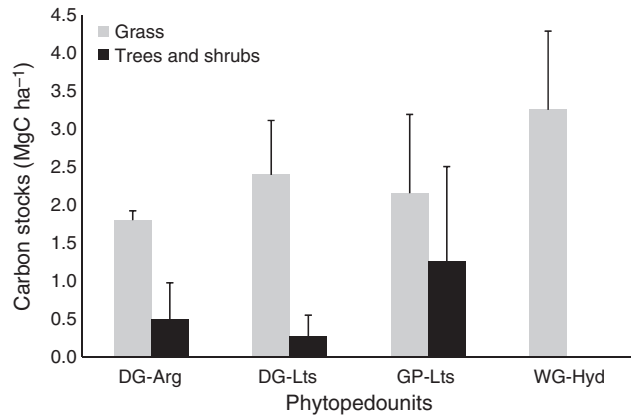


Fig. 2. Distribution of aboveground biomass carbon stock in two components (herbaceous and tree-bush) for the four phytopedounits sampled in open savannahs of Roraima, Brazil.

($3.47 \pm 0.89 \text{ MgC ha}^{-1}$) had the largest total aboveground carbon stock (Fig. 2). In this environment the tree-bush component represents a greater proportion of the biomass and has greater carbon content per unit of weight.

Belowground total biomass and carbon

The total biomass of roots determined for the 0–100-cm profile (direct + indirect method) of WG-Hyd ($29.52 \pm 7.15 \text{ Mg ha}^{-1}$) was greater as compared with the other phytopedounits studied (Table 2). The phytopedounits with tree-bush biomass all have the smallest values for root biomass. Fine roots (<2 mm) in diameter dominated the 0–100-cm vertical profile for the four open savannah phytopedounits evaluated in Roraima. The concentration of this category reached 100% in WG-Hyd and was between 92.5 and 97.9% in the other environments. The medium-diameter roots (2–10 mm) were found in three landscapes that

contained tree-bush biomass, with no significant differences being detected between these phytopedounits for this diameter category. Coarse roots ($\geq 10 \text{ mm}$) were determined only by the indirect method, with no concentration of this diameter class being detected by the direct (destructive) method.

The carbon content (%C) in the root biomass measured by the direct method varied from 24.8% in WG-Hyd, where herbaceous biomass predominated on sandy soil, to 31.7% in GP-Lts, which was the environment with the greatest presence of tree-bush biomass on clay soil (Table 3).

Vertical distribution

The vertical distribution of root biomass for the four phytopedounits evaluated in open savannahs of Roraima, measured by the direct method, followed a pattern of exponential decrease, with the greatest values in the 0–10-cm section, and smaller values in the subsequent sections (Fig. 3). The largest concentration of roots (fine and medium) was found in the first three sections of the vertical profile of the soil (0–30 cm), ranging from 56.0 to 64.6% in the four environments. Taking into consideration only these three sections of depth, the biomass of the roots of WG-Hyd was significantly different from the other environments that had a tree-bush component.

Root : shoot ratio (biomass and carbon)

WG-Hyd was the environment with the highest absolute root : shoot ratio, taking into consideration the total aboveground and belowground live biomass (Table 4). The values of the root : shoot ratios calculated on the basis of carbon were smaller than those calculated on the basis of biomass in all phytopedounits. Using only the carbon values for roots $\geq 2 \text{ mm}$ in diameter, the root : shoot ratio have the highest values in GP-Lts and DG-Arg (both with high tree-bush biomass).

Table 2. Distribution of root biomass (mean \pm s.d.) by diameter category (0–100 cm)

Different lowercase letters in each column indicate a distinct difference among values (Student–Newman–Keuls test; $P < 0.05$). See Table 1 for phytopedounit definitions

Phytopedounit	Fine roots (<2 mm) Mg ha ⁻¹	Medium roots (2–10 mm) Mg ha ⁻¹	Coarse roots ($\geq 10 \text{ mm}$) Mg ha ⁻¹	Total Mg ha ⁻¹
DG-Arg	20.27 \pm 1.39a	0.26 \pm 0.15b	0.87 \pm 0.72bc	21.40 \pm 2.47a
DG-Lts	22.14 \pm 1.47a	0.14 \pm 0.10b	0.33 \pm 0.33b	22.62 \pm 2.21a
GP-Lts	20.49 \pm 1.69a	0.39 \pm 0.15b	1.26 \pm 0.22c	22.14 \pm 4.90a
WG-Hyd	29.52 \pm 2.40b	0.00a	0.00a	29.52 \pm 7.15b

Table 3. Carbon content (%C) and total carbon stock (mean \pm s.d.) in roots of open savanna phytopedounits in Roraima, Brazil (0–100-cm depth)

Mean %C was calculated by weighting between direct and indirect methods. There is no significant difference between values with the same letter on each line (Student–Newman–Keuls test; $P < 0.05$). See Table 1 for phytopedounit definitions

Phytopedounit	Sub-total (direct method)		Sub-total (indirect method)		Total	
	MgC ha ⁻¹	%C	MgC ha ⁻¹	%C	MgC ha ⁻¹	%C
DG-Arg	6.28 \pm 0.29a	31.10 \pm 2.90	0.41 \pm 0.34bc	46.80	6.69 \pm 0.29a	32.06
DG-Lts	6.04 \pm 1.15a	27.03 \pm 2.63	0.21 \pm 0.14b	46.73	6.25 \pm 1.12a	27.69
GP-Lts	6.62 \pm 2.00a	31.73 \pm 4.10	0.58 \pm 0.10c	46.09	7.21 \pm 1.85a	32.89
WG-Hyd	7.10 \pm 1.65a	24.80 \pm 6.16	0.00a	–	7.10 \pm 1.65a	24.80

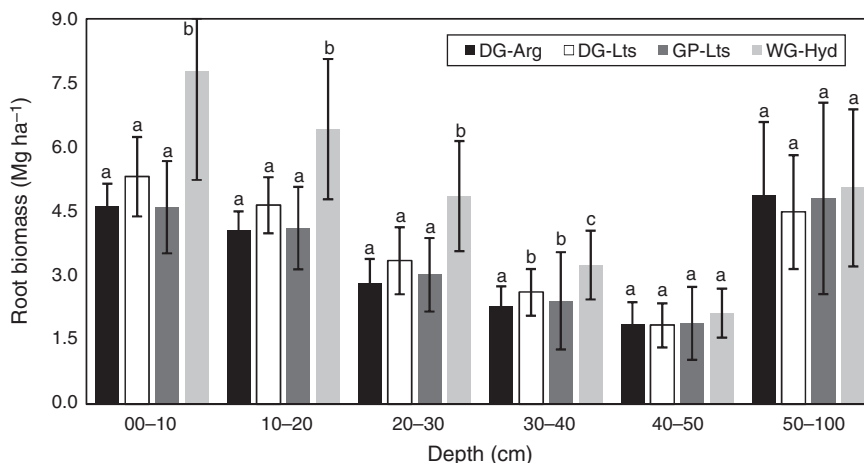


Fig. 3. Vertical distribution of root biomass (Mg ha^{-1}) by depth interval as estimated by the direct method (50–100 cm, calculated by exponential regression) in four open savannah phytotopedounits evaluated in Roraima. Values with the same letter in each depth interval have no significant difference between means, as determined by the Student–Newman–Keuls test ($P < 0.05$).

Table 4. Root : shoot ratio in different phytotopedounits sampled in open savannas of Roraima, Brazil for total (live) biomass and carbon, and separately for roots with ≥ 2 mm diameter

See Table 1 for phytotopedounit definitions

Phytotopedounit	Total		≥ 2 mm	
	Biomass	Carbon	Biomass	Carbon
DG-Arg	3.79	3.33	0.20	0.24
DG-Lts	3.48	2.64	0.07	0.08
GP-Lts	2.73	2.41	0.20	0.24
WG-Hyd	3.86	2.56	0	0

Discussion

Aboveground biomass and carbon

All of the environments evaluated had tree-bush biomass values within the expected range for open savannas in Roraima (0.05 – 3.64 Mg ha^{-1}) (Barbosa and Fearnside 2005b). However, our values for total herbaceous biomass are closer to the values found by Castro and Kauffman (1998) (6.0 – 7.5 Mg ha^{-1}) and Castro-Neves (2007) (6.2 – 10.4 Mg ha^{-1}) for *cerrado* areas near Brasília (in central Brazil) than to those found by Barbosa and Fearnside (2005b) for open savannas in Roraima (2.55 – 4.18 Mg ha^{-1}). Both studies in *cerrado* carried out their sampling at the peak of the dry period because they were interested in estimating the emission of greenhouse gases by burning. Our research took measures over the wet and dry periods to avoid biasing the mean for each environment. In the short term this method entails higher values for herbaceous biomass due to more favourable edaphic conditions in the wet season and even in the early months of the dry season, as in the case of WG-Hyd. This environment is characterised by the dominance of a grassy stratum that makes use of the soil moisture in order to expand its aboveground biomass. In the long term, savannah ecosystems where water availability is not limiting or that are protected from fire tend to increase their belowground biomass (Sarmiento 1984; San José *et al.* 1998).

Our results imply that, while the herbaceous and tree-bush components are heterogeneous amongst themselves, the results for aboveground total biomass and carbon of each phytotopedounit may be considered homogeneous, representing the same set of open savannah environments in Roraima. The phytophysionomic groups with low or average density of trees and bushes have total biomass and carbon that are similar to exclusively grassy environments under periodic flooding, regardless of the soil type.

Belowground biomass and carbon

Our values for total biomass of live roots (direct + indirect methods) for WG-Hyd are higher than the 11.4 – 18.9 Mg ha^{-1} presented by Sarmiento and Vera (1979) for savannah gradients between grasslands and woodlands in the Venezuelan *llanos* up to 2-m depth. However, despite differences in the sampling depth, more than 90% of the roots found in the study by Sarmiento and Vera are located in the top 60 cm, which is a value very close to 76–83% of our study to 50 cm. In contrast, the biomass of roots derived from studies in the *cerrado* of central Brazil is larger. Abdala *et al.* (1998) estimated a total value of 41.1 Mg ha^{-1} (live + dead) in a 6.2-m profile for a *cerrado* ‘sensu stricto’ on dark red latosol near Brasília, of which $\sim 23.3 \text{ Mg ha}^{-1}$ were in the first 50 cm (excluding the root crowns). Similarly, Castro and Kauffman (1998) found values ranging from 16.3 to 52.9 Mg ha^{-1} (2 m) for live roots in different savannah types ranging from grassland (*campo limpo* or ‘clean field’) to woodland (*cerrado denso* or ‘dense *cerrado*’), also located close to Brasília, with $\sim 80\%$ concentrated in the first 50 cm of depth.

Differences between our results for total belowground live biomass in Roraima and those for the *cerrado* of central Brazil are clearly due to sampling being performed at sites with different phytophysionomies, depths and burning schemes. Despite this contrast, it is possible to infer that, regardless of the depth or savannah type, the total biomass of live roots in areas of open savannah in Roraima with a low or medium presence of the tree-bush component are closer to those in the Venezuelan *llanos* than to those of the *cerrado* of central Brazil. This should be expected

since both the Venezuelan *llanos* and the open savannahs of Roraima have similar species composition, physiognomic structure, soil type and rainfall regime (San José and Fariñas 1983; Medina and Silva 1990; Miranda *et al.* 2002).

Another important inference is that the WG-Hyd phytopedonit, which is grassy and seasonally flooded, can have a large absolute increment in the biomass of live roots even in hydromorphic soils. This observation was also made by Menaut and Cesar (1979) when they investigated seven types of savannah in Lamto (Ivory Coast), also indicating that the biomass in wooded environments is almost always constant regardless of the density of trees. This contrasts with the general conclusions of Castro and Kauffman (1998) in the *cerrado* of central Brazil, indicating that dominance of aboveground woody biomass is reflected in increased belowground biomass. In our study, total carbon allocated to roots did not differ between the phytopedonits evaluated in open savannahs of Roraima, supporting the idea of uniformity among the open environments studied with low or no tree density.

The concentration of fine roots in the first layers of the soil in tropical savannah and grasslands is a pattern detected globally. Oliveira *et al.* (2005) observed that up to 1-m depth fine roots represented ~90% of the total determined for two types of *cerrado* (*campo limpo* 'grassland' and *campo sujo* 'scrubby savannah') in central Brazil. In a general review, Jackson *et al.* (1996) calculated 57% (9.90 Mg ha⁻¹) as the average proportion of fine roots in the upper 30 cm of soil in tropical savannahs and grasslands. Our study indicates that in open savannahs of Roraima these figures are higher in absolute terms and can reach values almost double the general average found by Jackson and collaborators for fine roots to 30-cm depth (11.5–19.1 Mg ha⁻¹ or 55–65% for the 0–100-cm profile).

The most significant example is the WG-Hyd savannah type, which is seasonally flooded and has 100% fine roots (<2 mm) throughout the sampled soil column. The plants in this type of environment are fully adapted to soils with sandy texture, periodic flooding and aluminium toxicity, but this savannah type has the largest biomass of roots even under these unfavourable edaphic conditions. In part, this expansion is explained by the prolonged maintenance of moisture in the soil in these phytopedonits even during the dry season. WG-Hyd has the largest concentration of roots between 0 and 10-cm depth (26.4%) and the lowest between 50 and 100-cm depth (17.1%), suggesting that the exploitation of nutrients in this soil is very superficial. Environments with greater presence of grasses are more efficient in absorbing water and nutrients in the upper soil layers because of the high concentrations of fine roots (Knoop and Walker 1985). In addition, sandy soils can also have a positive effect on root biomass increase as compared with soils with more clayey soil texture (Silver *et al.* 2000). Roots with smaller diameter have higher surface area relative to their size or weight and are more effective in capturing water and nutrients (Newman 1966; Vitousek and Sanford 1986). Nutrient-poor tropical environments therefore tend to have larger quantities of fine roots in the upper layers of the soil, with high rates of replacement (turnover rate), and better capacity to absorb nutrients (Jordan and Escalante 1980; Priess *et al.* 1999).

The larger-diameter roots (≥ 2 mm) are essential for the calculation of the total belowground biomass and carbon

stock, even in environments with low tree-bush density, as in the case of open savannahs in Roraima. The direct method allowed us to sample medium-diameter roots (2–10 mm) under conditions of lateral rooting. Adding this medium-root biomass to the biomass determined by the indirect method for coarse roots (≥ 10 mm) indicates that 0–7.5% (0–1.65 Mg ha⁻¹) of the total belowground biomass in savannahs with low tree-bush density in the far northern part of Amazonia is live roots with ≥ 2 mm diameter. In the more-wooded environments of the *cerrado* of central Brazil, the biomass of this component can reach values >20 Mg ha⁻¹ (Abdala *et al.* 1998; Castro-Neves 2007), depending on the tree-bush structure and density.

The smaller carbon content (%C) in roots found in the 0–50-cm soil column suggests a direct relationship with the large quantity of fine roots found in all of the savannah types studied. For example, Manlay *et al.* (2002) also found low values for carbon content (29.8–35.1% C) for fine roots under agricultural crops established in savannah areas in West Africa. Carbon content values lower than 40% are not common in the literature, but can be expected where the material analysed does not have lignified parenchyma. Fine roots are characterised as non-ligneous, almost all being without bark and with a short life cycle (McClougherty *et al.* 1982). These smaller-diameter roots die steadily throughout the year and quickly disappear from the system (Yavitt and Wright 2001) providing an important source of organic matter and mineral nutrients for maintenance and functioning of ecosystems (Luizão *et al.* 1992).

Gill and Jackson (2000) presented a range of 0.64–0.88 for the turnover rate in open environments in tropical zones (grasslands, shrublands and wetlands). Taking the midpoint of this range (0.76) and applying the results derived for the total carbon stock of roots in the phytopedonits evaluated in Roraima (Table 3), we estimate an annual carbon cycling on the order of 4.7–5.5 MgC ha⁻¹ (0–100 cm). In temperate forest ecosystems it is estimated that ~1/3 of this carbon is used in the production of new roots (Nadelhoffer and Raich 1992), but there are no estimates of this for tropical Amazonian savannahs and grasslands.

Vertical distribution

The distribution pattern of root biomass within the vertical soil profile observed in four phytopedonits was typically exponential with most of the roots concentrated in the surface layers. This pattern is the same as that observed in other studies of Neotropical savannahs and grasslands in northern South America (Sarmiento and Vera 1979; San José *et al.* 1982), in Central America (Kellman and Sanmugadas 1985; Fiala and Herrera 1988) and in the Brazilian *cerrados* (Abdala *et al.* 1998; Castro and Kauffman 1998; Delitti *et al.* 2001; Rodin 2004; Oliveira *et al.* 2005; Castro-Neves 2007; Paiva and Faria 2007). This is also an overall global pattern observed in other ecosystems where the great majority of roots is concentrated in the top 30 cm of the soil (Jackson *et al.* 1996; Schenk and Jackson 2002a).

In our case the extinction or decay coefficient (β) cannot be calculated using the formula of Gale and Grigal (1987) because our data were divided into 10-cm sections only up to 50-cm depth, whereas at least 100 cm would need to be so divided for a calculation of this type (see Jackson *et al.* 1996). However,

based on the decay pattern in the current data up to 30-cm depth, we suggest that all environments investigated have a superficial root distribution, with WG-Hyd (grassy environment on sandy soil) being most prominent ($\beta_{30\text{cm}} = 0.95$) as compared with tree-bush environments on clay soils ($\beta_{30\text{cm}} = 0.96$).

These values are lower than those given in the general review of Jackson *et al.* (1996) for the tropical savannah and grassland biome (0.972), but this could be a reflection of the small number of studies available at the time of the review (five in Africa, one in India and one in Cuba). Recent investigations in the *cerrado* of central Brazil found values of 0.97 (*cerrado stricto sensu*) and 0.99 (*campo sujo* 'shrublands') (Rodin 2004), and ranging from 0.88 to 0.92 for *cerrado stricto sensu* under different burning regimes (Castro-Neves 2007). This variation in values indicates that β is very variable and is highly dependent on the time of sampling (dry or wet season), soil type (clay or sand), drainage of the environment (hydromorphy) and phytophysionomy (grassy or different forms of wooded savannah).

Root : shoot ratio

Use of the root : shoot ratio as an indicator of the relationship between the belowground and aerial biomass (total live) is very important because it can serve as an estimator of belowground carbon based on a simple biometric survey of aboveground biomass with lower costs (Schenk and Jackson 2002b). Realistic root : shoot ratios are necessary to improve the accuracy of estimates of root biomass and to estimate the effects of management and land-use change in national inventories of greenhouse gas emissions (Mokany *et al.* 2006). In our study we calculate the root : shoot ratio based on biomass and carbon. This latter form provides ecological values closer to reality for calculation of stock, production and ecosystem productivity. This is because the carbon content (%C) of the different aboveground

components is not the same as that applied to belowground biomass. In ecosystems where the biomass of fine roots is overwhelmingly superior to the other categories, as in the case on the open savannahs of Roraima, the carbon content can be lower, causing the root : shoot ratio based on biomass to not represent the ecosystem faithfully.

The values of the root : shoot ratio based on total live biomass varied between 2.7 and 3.8, reflecting discrepancies between the total values above and below ground for all phytodunits. Higher ratios (3–5) were determined in the savannahs in Lamto (Ivory Coast), indicating greater total belowground biomass to a depth of 1 m as compared with aerial biomass (Menaut and Cesar 1979). However, these values are extremely variable and dependent on the depth of sampling. In the *cerrado* of central Brazil, Castro and Kauffman (1998) found high values for savannahs with low tree density (5.6–7.7) and smaller values for more wooded phytophysionomies (2.6–2.9) to 2-m depth, even without including any estimate for the biomass of the root crowns. Thus, although the phytodunits investigated in Roraima are limited by the low density of tree individuals, our values are closer to those of the wooded *cerrado* environments of Castro and Kauffman (1998) than to grassland environments. Our results indicate that the total biomass of roots (0–100-cm depth) is a component of great importance in the open savannah environments of Roraima, representing 2.4–3.3 times the total carbon allocated to aboveground biomass.

The IPCC (2006, p. 4.72) suggests that fine roots (<2 mm) are an integral part of the soil and, therefore, should be considered in the calculations of soil carbon. To have a valid correction for this it is necessary to disaggregate the results and use only the categories of roots ≥ 2 mm in diameter. This is required to prevent double counting of inventory values derived for soil carbon stocks. Thus, using our results for roots with diameter ≥ 2 mm for open savannah phytodunits studied in Roraima,

Table 5. Root : shoot ratio in the form used by the IPCC (ratio the biomass of roots ≥ 2 mm in diameter to live aboveground biomass) from the current study and recalculated from published studies on other Brazilian savannahs

Sa = open woodland; Sd = dense woodland; Sg = grasslands; Sp = savannah parkland

Phytophysionomy	IBGE legend ^A	Depth (m)	Root Mg ha ⁻¹ (≥ 2 mm)	Shoot Mg ha ⁻¹	R/S (≥ 2 mm)	Reference
<i>Cerrado Sensu Stricto</i>	Sa	6.2	21.40	34.58	0.62	B
<i>Campo limpo</i> (grassland)	Sg	2.0	11.57	2.90	3.99	C
<i>Campo sujo</i> (shrublands)	Sg	2.0	21.37	3.90	5.48	
<i>Cerrado Sensu Stricto</i> (open cerrado)	Sa	2.0	33.02	17.60	1.88	
<i>Cerrado Sensu Stricto</i> (dense cerrado)	Sd	2.0	37.56	18.40	2.04	
<i>Cerrado Sensu Stricto</i> (biennial precocious)	Sa	0.5–1.0	38.15	21.00	1.82	D
<i>Cerrado Sensu Stricto</i> (biennial modal)	Sa	0.5–1.0	43.61	29.00	1.50	
<i>Cerrado Sensu Stricto</i> (biennial late)	Sa	0.5–1.0	39.18	22.90	1.71	
<i>Cerrado Sensu Stricto</i> (quadrennial)	Sa	0.5–1.0	39.86	26.30	1.52	
Dry grassland (Argisol)	Sg	1.0	1.14	5.65	0.20	E
Dry grassland (Latosol)	Sg	1.0	0.47	6.50	0.07	
Mosaic grasslands/shrublands (Latosol)	Sg/Sp	1.0	1.65	8.10	0.20	
<i>Campo úmido</i> (Hydromorphic)	Sg	1.0	0.00	7.65	0.00	

^ABrazilian vegetation classification code determined by IBGE (1992).

^BAbdala *et al.* (1998); includes live and dead roots.

^CCastro and Kauffman (1998); does not include tap roots. These authors considered fine roots to be <6 mm diameter. The biomass of roots <2 mm was estimated as 29% of the total of roots in a 2-m profile according to Abdala *et al.* (1998).

^DCastro-Neves (2007); uses Abdala *et al.* (1998) for calculation of coarse roots (0–100 cm) and a direct method for estimating fine roots up to 50-cm depth.

^EThis study.

the root : shoot ratio, based on biomass, is between 0 (seasonally flooded grasslands) and 0.07–0.20 (grasslands with low tree density), or between 0 and 0.08–0.24, based on carbon (see Table 4). These values are lower than those indicated as the default values by the IPCC (2003, p. 3.109, table 3.4.3; IPCC 2006, p. 6.8, table 6.1) for sub-tropical/tropical grassland (1.6), woodland/savannah (0.5) and shrubland (2.8). However, the IPCC strongly suggests that default values only be used when the country does not have regional values that better reflect the ecosystem (IPCC 2006, p. 6.8).

The second Brazilian inventory used the default values for all grassland and savannah environments as listed in Brazil MCT (2010, pp. 236–237). This was done both for the *cerrados* of central Brazil (for which published estimates of belowground biomass existed) and for Amazon savannahs (for which the present study provides the first estimates). Although few in number, it is possible to make inferences about the root : shoot ratio for Brazilian savannahs, including *cerrados* (Table 5). For example, the Brazilian estimates for root : shoot ratio (roots ≥ 2 mm) vary tremendously depending on the vegetation type, fire regime, seasonality of the watertable, soil class and sampling depth. Environments in central Brazil with greater aboveground biomass and that are not influenced by the watertable have root : shoot ratios from 7 to 27 times higher than those in Amazonian grasslands and savannahs with low arboreal biomass.

We therefore propose a reformulation of the calculations for the next Brazilian national inventory. We suggest a minimum standardisation of 1-m depth for the estimates of belowground biomass and carbon, in addition to region-specific values for root : shoot ratios, with different ratios, for Amazonian grasslands/savannahs and for central Brazilian *cerrados*. This calculation strategy would bring advantages in avoiding the use of empirical default values from the IPCC (2003, 2006), thereby providing more realistic values for total biomass and carbon for ecosystems with open vegetation in Brazil.

Conclusions

The total biomass of roots of seasonally flooded grasslands is higher than the root biomass of grasslands with low tree-bush density, although the total belowground carbon stock does not differ among phytodoundunits.

The vertical distribution pattern of root biomass follows an exponential model, with the largest concentration of roots being in the more superficial layers of the soil. This pattern does not differ among phytodoundunits.

The total biomass of roots (direct + indirect methods) in open savannah environments of Roraima represents a pool 2.4–3.3 times the total carbon stocked in aboveground biomass.

The expansion factor (root : shoot ratio) used by IPCC for belowground biomass in roots ≥ 2 mm diameter, starting from live aboveground biomass, is zero for seasonally flooded grasslands of Roraima (in northern Amazonia). For unflooded grasslands with low densities of trees the values of this factor range from 0.07 to 0.20 on a biomass basis, or from 0.08 to 0.24 on a carbon basis.

The standardisation of the minimum sampling depth and the use of region-specific values for root : shoot ratios to

calculate belowground biomass in grasslands and savannahs is advantageous because it provides more realistic values of total biomass and carbon.

Supplementary material

Supplementary material with details regarding the carbon concentration (%C) of the main tree and shrub species, and density (number ha⁻¹) and basal area (cm² ha⁻¹) of the tree-bush component present in the phytodoundunits is available from the Journal's website.

Acknowledgements

We thank the Federal University of Roraima and the Brazilian Enterprise for Agriculture and Ranching Research for permission to use the Research Program on Biodiversity grids installed in their experimental stations. The project was financed by the Institutional Research Program of the National Institute for Research in the Amazon (PPI/INPA-PRJ 012/18), linked to the CNPq research group 'Ecology and Management of Natural Resources of Savannahs of Roraima' and INCT-Servamb (MCT). CAPES granted postgraduate scholarships (Masters degree) to J.R.S. Santos and M.S. Cunha. CNPq granted productivity fellowships to R.I. Barbosa and P.M. Fearnside.

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