



The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests



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ABSTRACT

Accurate measures of plant biomass and productivity are important to predict the impacts caused by current anthropogenic changes in the carbon pool. Changes in the carbon pool may be decisive whether plant communities act as sinks or sources for carbon dioxide. However, there are not accurate assessments of savanna and seasonal forest biomass, particularly belowground, which is essential to evaluate their carbon stock. We tested whether we could use soil variables, fire frequency, topography, and functional traits to build simple models to predict the belowground system in savanna and seasonal forest. In central Brazil, we collected root biomass up to 100 cm deep and annual fine root productivity in the top 40 cm of soil with an ingrowth donut, in 100 plots in savanna and 20 plots in seasonal forest. We used increasing complexity general linear modeling to find the models predicting the root biomass and productivity. We found significant models in all cases, even though the explanatory power for the savanna was low. The main ecological forces related to the root biomass and productivity were soils poor in nutrients, foraging for potassium in the savanna and for nitrogen in the forest, drought, resistance to disturbance, and niche complementarity. Reliable estimates of root biomass might be used to replace direct but laborious excavation methods. The carbon stock of savanna and seasonal forest are large and should not be neglected when estimating the impacts caused by climate and land-use changes.

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1. Introduction

Plant biomass and net primary production, that is, the build-up of plant biomass that feeds the entire community food web, are ecological properties important for biogeochemical cycles (Balvanera et al., 2006). Changes in plant biomass and, thus, in the carbon pool, may be decisive whether plant communities act as sinks or sources for carbon dioxide (Fearnside, 2000; Tilman et al., 2001). On the one hand, deforestation releases a large amount of carbon to the atmosphere (Castro and Kauffman, 1998). On the other hand, plant communities may mitigate climate change through carbon sequestration and enhance carbon storage in the short term (Myneni et al., 2001). In the long term, residence time of the carbon and, thus, community dynamics will be determining to the carbon storage in plant biomass (Körner, 2003). Thus, accurate measures of plant biomass and productivity are important to predict the impacts caused by current anthropogenic changes in the carbon pool (Fearnside and Laurance, 2004).

A great part of the plant biomass, and consequently a large amount of the carbon pool, is allocated to the root system (Robinson, 2007). Thus, it is important to obtain information on root biomass to predict the effect of deforestation on global warming (Fearnside and Laurance, 2004). However, root biomass is often underrepresented due to the difficulty in obtaining belowground data (Mokany et al., 2006). Not only are studies on root biomass lacking, but also on root productivity, which accounts for 75% of the total net primary production and has a great impact on the carbon cycle (Gill and Jackson, 2000). Root productivity is a prerequisite for nutrient foraging and water uptake, also providing a primary input of organic carbon and nutrients to the soil via root turnover (Pärtel et al., 2012; Price et al., 2012). The main parts of the root system responsible for nutrient and water uptake are fine roots, those with less than 2 mm diameter, which occur in greater density than coarse roots in the cerrado (Casper and Jackson, 1997; Castro and Kauffman, 1998).

Two of the most unknown biomes concerning root biomass due to lack of replicates or unverifiable sampling methods are savannas and tropical forests (Mokany et al., 2006). These biomes occur side by side within the Brazilian cerrado domain, one of the hotspots for biodiversity conservation in the world (Myers et al., 2000).

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The cerrado domain comprises the cerrado vegetation, which ranges from grassland to tall woodland, but most of its physiognomies fit the definition of savanna (Gottsberger and Silberbauer-Gottsberger, 2006). Other vegetation types occur within the cerrado domain, including tropical forests, such as the semideciduous seasonal forest, which grows on richer soils (Gottsberger and Silberbauer-Gottsberger, 2006). Since the cerrado domain originally occupied more than 2 million km², an area larger than, for example, Mexico, climate and land-use changes in that domain may cause a global impact on carbon cycling (Ratter et al., 1997). For instance, high deforestation rates of the cerrado in the last 50 years have been diminishing dramatically the amount of carbon stored in plant biomass, releasing it to the atmosphere (Ratter et al., 1997; Castro and Kauffman, 1998).

In other savannas and tropical forests, 80% of the root biomass is in the top 100 cm of the soil (Jackson et al., 1996; Castro and Kauffman, 1998). According to the data available, savannas have root biomass of 15 Mg ha⁻¹ and root:shoot ratio of 0.7 (Jackson et al., 1996). In the cerrado, the savanna sites have particularly high root biomass, between 30 and 53 Mg ha⁻¹ (Castro and Kauffman, 1998; Liliensein et al., 2001), and root:shoot ratio ranges from 0.6 to 2.9 (Ribeiro et al., 2011), that is, in some areas, most biomass is allocated belowground. In tropical forests, root biomass is 40 Mg ha⁻¹ and root:shoot ratio is lower than in savannas, from 0.2 to 0.3 (Jackson et al., 1996). In savannas, root productivity ranges from 4 to 8.3 Mg ha⁻¹ y⁻¹ (Pandey and Singh, 1992), whereas, in tropical forests, it goes from 1.7 to 7.6 Mg ha⁻¹ y⁻¹ (Aragão et al., 2009).

The lack of information on the root system is partly caused by the difficulty in obtaining data (Milchunas, 2009). Different approaches have been suggested to assess belowground biomass and productivity, and most of them include excavation or costly methods, as isotope decay and minirhizotron (Milchunas, 2009). Instead of excavating and directly measuring root biomass and productivity, one might estimate root biomass in large areas using regression models with commonly available abiotic and biotic variables (Díaz et al., 2007).

In the cerrado, environmental filters limit species occurrences and biomass production (Gottsberger and Silberbauer-Gottsberger, 2006). The savanna physiognomies of the cerrado vegetation occur on more acid, poorer, and better drained soils when compared to the semideciduous seasonal forest (Ruggiero et al., 2002). Less fertile soils, with less organic matter and nutrient content, should be related to higher root biomass, increasing the nutrient uptake (Tateno et al., 2004). Also, fire is a recurrent event impacting the species composition and biomass production (Bond and Keeley, 2005). Most cerrado species have coarse subterranean organs that allow them to resist and survive fires, used to resprout (Coutinho, 1990). Topography affects water availability, changing the depth of the ground water level (Rossatto et al., 2012). Ground water approaches the surface in lower areas, increasing water availability during the dry season, but decreasing the volume of soil available to root growth (Rossatto et al., 2012). In the cerrado domain, poorer soils, higher fire frequencies, and lower water availability, due to seasonal rainfall or access to the water table, are expected to be related to higher root:shoot biomass.

Besides the abiotic filters, biotic features may also be related to the plant biomass (Díaz et al., 2007). For instance, functional traits may change plant fitness and survival, affecting biomass productivity (Tilman et al., 1997). In the cerrado, functional traits that allow better use of soil resources, higher fire resistance, and higher water uptake from the water table at fine spatial scale should allow higher biomass production (Tilman et al., 1997; Cardinale et al., 2006). Moreover, higher functional diversity may lead to different use of resources and higher productivity (Tilman et al., 1997). Indeed, functional diversity has been shown to impact several

community processes, such as aboveground productivity and decomposability of organic matter (Klump and Soussana, 2009).

We aimed to improve the estimation of root biomass and productivity of savanna and tropical forests, two of the most unknown biomes concerning the belowground system. Not only did we use environmental variables, but also functional traits related to stress resistance and plant fitness to test whether we could build a general and simple model to predict root biomass and productivity in the cerrado domain, avoiding, thus, excavation methods.

2. Material and methods

We carried out this study in Emas National Park, central Brazil, at 17°49'–18°28'S and 52°39'–53°10'W, from October 2009 to December 2011. The park has an area of 132,941 ha and its climate is Aw (Köppen, 1931), with dry winters and rainy summers. Average rainfall ranges from 1200 to 2000 mm year⁻¹, concentrated between September and March, and annual mean temperature is 24.6 °C (Ramos-Neto and Pivello, 2000). Soils are mostly Oxisols and the bedrock is composed of a variety of Pre-Cambrian gneisses and granites (França et al., 2007). The vegetation in the park is dominated by savanna, with varying tree density (França et al., 2007). Other vegetation types, such as semideciduous seasonal forest, occur in small patches within the reserve. In the savanna physiognomies, we established 100 5 m × 5 m plots using a stratified random sampling design (Krebs, 1998). The sampling comprised 10 categories of fire occurrence, with 10 plots in each category, from the absence of fire to annual fire in the last 16 years. In the semideciduous seasonal forest, due to the small size of the patches and to the absence of fire, we placed 20 5 m × 5 m plots, 50 m apart one from the other, in a regular grid.

In each of the 120 plots, we had one sample of root biomass to the depth of 100 cm, including roots from trees, shrubs, and grasses. In the upper 40 cm, we extracted soil monoliths of 40 × 40 cm. From 40 to 100 cm deep, we extracted a core using an auger of 30 cm diameter (Castro and Kauffman, 1998). We did not sample any tree stumps, so the overall root biomass might have been underestimated. We sieved the soil with a mesh of 2 mm and washed the roots to eliminate soil particles. We dried the roots in the oven at 70 °C for 48 h and weighed them. We extrapolated root biomass to one hectare to make it comparable with other studies. We assessed root productivity for fine roots (<2 mm diameter) in the upper 40 cm with an ingrowth donut method (Milchunas et al., 2005), placing 96 cores in the savanna and 16 in the seasonal forest. We established the cores between November and December 2010 and measured the root biomass produced after one year, including live and dead roots. The cores had a diameter of 20 cm and a depth of 40 cm, and the area where root ingrowth occurred was 2.5 cm wide. The soil samples used to fill the cores were taken from the same plot, and the horizons were kept intact. The mesh limiting the outside of the cores was made of rigid plastic with holes of 2 mm × 2 mm, restricting the growth to fine roots (Milchunas et al., 2005).

In each plot, we collected soil samples in the top 5 cm of soil, the layer most correlated to the vegetation structure in the cerrado (Ruggiero et al., 2002). For each sample, we measured: pH, organic matter, total nitrogen, phosphorus, potassium, calcium, magnesium, aluminum, sum of bases, cation exchange capacity, base saturation, aluminum saturation, and the proportions of clay, silt, and sand. Soil analyses followed the procedures described by Rajj et al. (1987) and Silva and Batalha (2008). Soil pH was determined in CaCl₂ solution, organic matter was determined by organic carbon oxidation with potassium dichromate and following potassium dichromate titration with ammoniac ferrous sulfate. Total nitrogen was assessed by digestion with H₂SO₄ and distillation with NaOH. Available phosphorus was evaluated by spectrophotometry after

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