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 km^2, 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; Lilienfein 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 (Klumpp 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 Raij et al. (1987) and Silva and Batalha (2008). Soil pH was determined in CaCl$_2$ solution, organic matter was determined by organic carbon oxidation with potassium dichromate and following potassium dichromate titration with ammonic ferrous sulfate. Total nitrogen was assessed by digestion with H$_2$SO$_4$ and distillation with NaOH. Available phosphorus was evaluated by spectrophotometry after

anion exchange resin extraction. The cations K^+, Ca^{+2}, Mg^{+2}, and Al^{+3} were extracted with KCl. Potassium, calcium, and magnesium were determined by an EDTA complexometry measurement. Aluminum was determined by NaOH titration. Sum of bases was calculated as the sum of potassium, calcium, and magnesium. Cation exchange capacity was considered as sum of bases plus H^+ and Al^{+3} concentrations. Base saturation was computed as a percentage of total cation exchange capacity. Aluminum saturation was a percentage of sum of bases and Al^{+3}. We quantified soil sand, silt, and clay proportions using the Boyoucos method (Silva and Batalha, 2008). To assess fire history, we had two variables based on satellite images, from 1984 to 2010: years elapsed since last fire and mean interval between fires in each plot. As surrogates for water availability, we measured altitude with an altimeter and slope with an inclinometer. In Emas National Park, the higher and the flatter is the area, the deeper the groundwater (Rossatto et al., 2012).

Within each plot, we identified all woody individuals with stem diameter at soil level larger than or equal to 3 cm. To each individual, we sampled performance and functional traits, hereafter called 'functional traits' (Pérez-Harguindeguy et al., 2013). The functional traits were: basal area, tree height, bark thickness, wood density, specific leaf area, leaf size, leaf toughness, leaf nitrogen content, leaf phosphorous content, and leaf potassium content. Basal area, tree height, bark thickness, and specific leaf area are related to disturbance and are expected to differ according to fire regimes (Dantas et al., 2013). Wood density and leaf size are responsive to disturbance and soil nutritional content, indicating competitive strength (Pérez-Harguindeguy et al., 2013). Leaf toughness is related to nutrient availability in soil and plays a role avoiding herbivores (Pérez-Harguindeguy et al., 2013). Leaf nutrients are related to disturbance and to the availability of nutrients in soil that limit plant growth (Pérez-Harguindeguy et al., 2013). We included top kill and tortuosity of the main branch as measures of resprout ability and fire resistance (Higgins et al., 2007). Top kill is a binary trait, present when the aboveground part of the tree died and resprouted from the root system (Hoffmann et al., 2009). Tortuosity is the length:height ratio up to the first bifurcation and describes how straight the main stem of the tree is. High tortuosity is a response to high disturbance level, such as fire and drought (Eiten, 1972). For each trait sampled, we assessed the community weighted mean value, which is the mean of the trait accounting for species abundances (CWM, Garnier et al., 2004) and the divergence of the traits, using Rao's quadratic diversity index (FD$_Q$, Rao, 1982; Ricotta and Moretti, 2011).

We followed a two-stage method suggested by Díaz et al. (2007) to obtain predictive models to root biomass and productivity using abiotic and biotic variables (Fig. 1), but not including species abundances and discontinuous effects, as originally proposed. We added the variables in an increasing complexity general linear model, which reduces the uncertainty in predicting ecological processes (Díaz et al., 2007). We excluded from the analyses soil variables that were highly correlated to others (Pearson's $r > |0.7|$), maintaining as few variables as possible. Functional traits were not highly correlated among them or to the soil variables, so we kept them all in the analyses. When necessary, data were log-transformed to reach normality.

In the first stage, we tested for the effect of abiotic and biotic factors on root biomass and productivity separately. In the first step, we tested the effect of the abiotic variables. Soil variables analyzed were pH, organic matter, nitrogen, phosphorus, potassium, calcium, magnesium, and aluminum content, cation exchange capacity, and the proportions of clay and silt. Also, we included time since last fire, mean fire interval, altitude, and slope. Then, we tested for the effect of functional traits, using the community weighted mean (Garnier et al., 2004) and the dispersion of each trait (Rao, 1982). In each step, significant factors were identified and in the second stage, they were added and kept when they improved the model fitness. We selected the best models by parsimony (Díaz et al., 2007, Fig. 1). We also ran the analysis with standardised values to assess the weight of each variable in the regression models (see Electronic Supplementary Material).

3. Results

Root biomass of the first 100 cm deep in the savanna was 29.8 ± 21.7 Mg ha^{-1} and 38.3 ± 28.4 Mg ha^{-1} in the seasonal forest. Fine root productivity was 98.9 ± 41.5 g m^{-2} year^{-1} in the savanna and 71.4 ± 26.6 g m^{-2} year^{-1} in the seasonal forest. Among the abiotic variables, we excluded from the analysis those soil variables that were highly correlated to other variables, which were sum of bases, base saturation, aluminum saturation, and sand proportion. Sum of bases was correlated with potassium ($R = 0.71$), calcium ($R = 0.91$), and magnesium ($R = 0.91$); base saturation
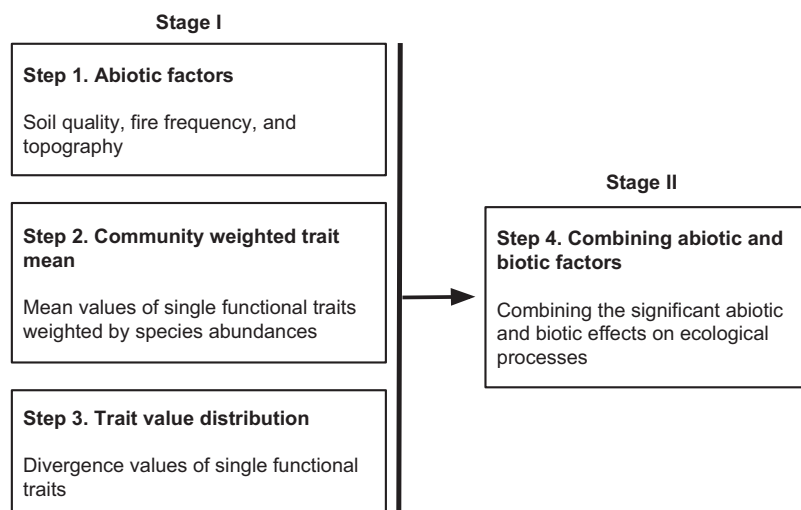
Stage I

Step 1. Abiotic factors

Soil quality, fire frequency, and topography

Step 2. Community weighted trait mean

Mean values of single functional traits weighted by species abundances

Step 3. Trait value distribution

Divergence values of single functional traits

Stage II

Step 4. Combining abiotic and biotic factors

Combining the significant abiotic and biotic effects on ecological processes

Fig. 1. Steps to predict root biomass and productivity in the savanna and in the seasonal forest in Emas National Park, central Brazil, following Díaz et al. (2007). In the first stage, we tested for relationships of each variable separately with root biomass and productivity. In step 1, we used abiotic variables, that is, soil features, fire frequency, and topography. In steps 2 and 3, we used, respectively, community weighted mean (CWM, Garnier et al., 2004) and functional divergence (FD$_Q$, Rao, 1982) of 12 functional traits related to disturbance resistance. In the second stage, we added significant factors from steps 1–3 and kept them when they improved model fit following Akaike's criterion.

was correlated with calcium ($R = 0.88$) and magnesium ($R = 0.89$); aluminum saturation was correlated with calcium ($R = 0.93$) and magnesium ($R = 0.90$); and sand proportion was correlated with silt proportion ($R = 0.98$). We measured the functional traits from 531 individuals belonging to 55 species in the savanna and from 185 individuals belonging to 43 species in the seasonal forest.

We found significant models to predict root biomass and productivity in the savanna and in the seasonal forest ($P < 0.05$ in all cases). In the first stage of the analysis, we assessed the significant variables, when taken separately into account (Table 1). In the second stage, we built the final models, excluding by parsimony some of the significant variables found in the first stage (Table 2). In the savanna, root biomass was related to low altitude, low tortuosity, low leaf potassium content, and high divergence of leaf toughness ($R^2_{adj} = 0.24$, Table 2). In the seasonal forest, root biomass was related to low clay proportion, low bark thickness, and high leaf nitrogen content ($R^2_{adj} = 0.56$, Table 2). In the savanna, root productivity was related to low clay content, high organic matter, low leaf potassium content, and high divergence of bark thickness ($R^2_{adj} = 0.16$, Table 2). In the seasonal forest, fine root productivity was related to leaf nitrogen content and top kill ($R^2_{adj} = 0.55$, Table 2). The models with standardised variables showed similar contributions of each variable (see Electronic Supplementary Material).

4. Discussion

In the savanna we studied, we found similar root biomass that was found in the savanna physiognomies of the cerrado by other authors (Castro and Kauffman, 1998; Lilienfein et al., 2001), which is twice as much as reported in other savannas in the world (Jackson et al., 1996). Root biomass in the cerrado represents larger share of the carbon pool than expected by extrapolation from other savannas (Jackson et al., 1996; Grace et al., 2006). Hence, the high rates of deforestation, changes in climate and in land-use in the cerrado region will have greater impact on the global carbon balance than expected (Jackson et al., 1996; Grace et al., 2006). In

the seasonal forest, root biomass and productivity were larger than we found in savannas, but similar to those found in other tropical forests (Jackson et al., 1996; Aragão et al., 2009). Nonetheless, root biomass in savannas might have been relatively larger than we report here in comparison to tropical forests, if we had considered deeper layers of soil than one meter (Jackson et al., 1996). The rapid deforestation of tropical vegetation is a major source of greenhouse gases (Fearnside and Laurance, 2004). In this sense, updating the expectations of the belowground carbon pool to the cerrado domain will increase the accuracy of estimates of the impacts caused by changes in climate and land-use (Fearnside, 2000).

Root biomass and productivity in the savanna and the seasonal forest could be predicted to a variable extent by using abiotic and biotic variables. All of our models were significant, even though they had a lower explanatory power in the savanna. Excluding functional traits of the herbaceous understory vegetation might have been responsible for this reduced power. Savannas have an almost continuous herbaceous layer, which represents more than half of the plant species (Scholes and Archer, 1997). If we had sampled the herbaceous layer as well, explanatory power of the savanna models could have been increased and other ecological processes related to root biomass production could have been identified. In the semideciduous seasonal forest, where the herbaceous layer is less important than in the savanna, models were simpler and had a better fit. However, data on functional traits on the herbaceous layer in tropical vegetation is not widely available, and models including herbaceous functional traits would be hardly applied to predict the belowground carbon pool (Gottsberger and Silberbauer-Gottsberger, 2006). Despite the lower explanatory power of the savanna models, we found variables related to the root biomass and productivity, suggesting ecological processes underlying them.

Communities under low disturbances, with better soil quality and better access to ground water, were more productive, suggesting that they are controlled by interactions between water and nutrient availability (Bustamante et al., 2012). Low clay proportion,

Table 1
Stage I of the analyses relating abiotic and biotic variables to root biomass and fine root productivity in savanna and seasonal forest, Emas National Park, central Brazil, following Díaz et al. (2007). The list of all functional traits analyzed is presented in the methods. The + and − signs indicate whether the correlation was positive or negative. We show only significant relationships ($P < 0.05$). OM: organic matter, CWM: community weighted mean.

Stage I	Step 1: abiotic variables		Step 2: CWM		Step 3: trait divergence	
	Variable	P	Variable	P	Variable	P
Savanna root biomass	− Altitude	0.01	− Tortuosity	0.01	+ Leaf toughness	0.01
	− Clay	0.03	− Leaf potassium	0.01	−	−
Forest root biomass	− Clay	0.04	− Leaf toughness	0.01	−	−
	−	−	+ Leaf nitrogen	0.02	−	−
	−	−	− Bark thickness	0.04	−	−
Savanna root productivity	+ OM	0.01	− Leaf potassium	0.03	+ Bark thickness	0.01
	− Clay	0.01	−	−	−	−
Forest root productivity	−	−	− Top kill	0.003	−	−
	−	−	− Leaf nitrogen	0.009	−	−

Table 2
Final models predicting root biomass and productivity in the savanna and in the seasonal forest, and the variability explained by each model (R^2_{adj}, Díaz et al., 2007). Data were log-transformed when necessary to reach normality. The + and − signs before the variables indicate whether the correlation with root biomass or productivity was positive or negative. All models were significant ($P < 0.05$).

Response variable	Explanatory variables	R^2_{adj}
Ln (root biomass savanna)	10.65−0.05 altitude − 2.95 tortuosity − 0.07 leaf potassium + 0.05 leaf toughness divergence	24
Ln (root biomass seasonal forest)	5.87−0.004 clay − 0.24 bark thickness + 0.10 leaf nitrogen	56
Ln (root productivity savanna)	1.75−0.006 clay + 0.006 OM − 0.02 leaf potassium + 0.11 bark thickness divergence	16
Ln (root productivity seasonal forest)	3.62−0.08 leaf nitrogen − 4.01 top kill	55

high organic matter content, and low altitude were related to high root biomass and productivity. Extremely clayey soils, that are poorly permeable, may diminish the penetration of nutrients and water to deeper layers, limiting the soil volume available to root growth, as we found in savanna and seasonal forest (Schenk and Jackson, 2002; Rossatto et al., 2012). Organic matter is an important cation exchanger, and fine roots have a central role in the cation uptake (Gottsberger and Silberbauer-Gottsberger, 2006; Price et al., 2012). The higher availability of cations in the soil was related to larger fine root productivity in the savanna, probably increasing the cation uptake (Forde and Lorenzo, 2001). Lower altitude approximates the ground water to the soil surface (Rossatto et al., 2012), increasing plant access to water during the dry season and, consequently, biomass production (Oliveira et al., 2005; Sankaran et al., 2005). In this sense, poor soils and drought were the most important filters limiting root growth in the savanna, whereas poor soil was the only filter in the seasonal forest.

Contrary to our expectation, difference in the fire frequency was neither correlated to root biomass nor productivity. Fire is expected to be an important factor altering carbon and nutrients stocks and fluxes in the cerrado domain (Bustamante et al., 2012). However, the belowground carbon stocks are more conservative in response to fires than the aboveground stock, and it might be necessary to include a longer time scale to observe such effects in the belowground layer (Bustamante et al., 2012). Fire has been occurring in the cerrado vegetation for at least 20 million years (Simon et al., 2009; Simon and Pennington, 2012), and most species are able to store carbohydrates in the root system and resprout after fire. At short time scales, there is a functional stability in the root system under different fire frequencies, possibly due to the same root-growth strategy. Additionally, fine and coarse roots might have different responses to fire. Successive burning at the longer time scale promotes tree mortality, decreasing coarse root biomass, and favors grass cover, increasing fine root biomass (Bustamante et al., 2012). If so, a different pattern may be found if longer time scale and different root thicknesses are analyzed.

Among the biotic variables, some functional traits were related to root biomass production. Low tortuosity in savanna and low bark thickness or top killing in the seasonal forest were related to higher root biomass or productivity. Tree tortuosity is common in the cerrado and may be a consequence of frequent fires, nutrient-poor soils, or water deficiency (Eiten, 1972). Tortuosity is not often measured since it does not appear in sampling protocols of traits related to disturbance (for example, Cornelissen et al., 2003 and Pérez-Harguindeguy et al., 2013). Nonetheless, tree tortuosity was related to root biomass and should be considered in future studies in savannas. Bark thickness is responsive to soil nutritional quality and water availability, and to fire at the evolutionary scale, whereas top killing is responsive to high fire frequency (Cornelissen et al., 2003; Hoffmann et al., 2009) and were negatively related to root biomass in the seasonal forest. As a general trend, functional traits responding to low disturbances were related to higher carbon stock, as we expected (Di Iorio et al., 2011).

Even though cerrado species have low variability in leaf nutrient concentration due to nutrient limitation in the soil (Cianciaruso et al., 2013), leaf potassium and leaf nitrogen were related to root biomass and productivity in the savanna and in the seasonal forest, respectively. Potassium has a role in enzyme functioning, controls the water cellular balance, and is highly mobile within the plant (Prado, 2013). Leaf nitrogen is related to relative growth, photosynthetic rate, and to the nitrogen availability in the environment (Cornelissen et al., 2003). In the seasonal forest, low leaf nitrogen total content was related to low root biomass, but to high root productivity. Nitrogen was negatively related to total root biomass, as expected (Ladwig et al., 2011), but increased the productivity of fine roots, which are responsible

for foraging and nutrient uptake (Price et al., 2012). Nitrogen variability was related to the root biomass with different effects on the standing root biomass pool and on the root productivity. Potassium and nitrogen availability are related to root production, possibly increasing the uptake of limiting resources (Price et al., 2012), and they were also related to the root biomass and productivity in the cerrado.

Additionally, high divergences of leaf toughness and bark thickness were positively correlated to root biomass and productivity in the savanna, but not in the seasonal forest. High divergence is a consequence of extreme values of functional traits, especially among the most abundant species (Villéger et al., 2008). Functional divergence shifts due to changes in the intensity of competitive interactions and, thus, in species similarity (Mason et al., 2007). High competition between species might lead to niche differentiation and thus high trait complementarity and dissimilar use of resources, increasing biomass production (Tilman et al., 1997; Villéger et al., 2008). Carbon pool and productivity have been affected by competition-driven changes in functional traits, besides the effects of abiotic variables (Price et al., 2012). Low disturbance levels, foraging for potassium in the savanna and for nitrogen in the seasonal forest, and presumably greater complementarity among species were related to higher root biomass and productivity in our study.

In our models, we excluded from our analysis the fourth step suggested by Díaz et al. (2007), which tests for the relationship between species abundances and the ecological properties studied. Some of the species abundances had been related to root biomass and productivity and their inclusion would have increased model fit (see Electronic Supplementary Material). Nevertheless, tropical communities have high beta diversity and, therefore, species composition and abundances change greatly from site to site (Gottsberger and Silberbauer-Gottsberger, 2006). As one of our aims was to produce models to estimate the carbon pool and productivity that could be applied to other sites within the cerrado domain, we chose not to include species abundances (Gottsberger and Silberbauer-Gottsberger, 2006). Moreover, it was not necessary to search for discontinuous effects, the last step proposed by Díaz et al. (2007), because all our models were significant.

There are few examples in the literature combining abiotic and biotic effects to explain ecological processes, especially with field data and in the Tropics (Balvanera et al., 2006). The predictability of the models proposed here might be improved by including traits of herbaceous species, especially in the savannas. In conclusion, we found that root biomass in cerrado is related to soils poor in nutrients, foraging for potassium in the savanna and for nitrogen in the forest, drought, resistance to disturbance, and niche complementarity. Deforestation of tropical vegetation is a major source of greenhouse gases, and predicting the belowground stock of carbon in cerrado is of great importance to estimate and minimize the impacts caused by the loss of natural areas (Bustamante et al., 2012). The root system comprises an important share of the carbon pool of the cerrado domain, larger than previously expected for the savannas, and should not be neglected when estimating the impacts caused by climate and land-use changes.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.01.014.

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