

# Disentangling the roles of resource availability and disturbance in fine and coarse root biomass in savanna

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**Abstract** Savannas are among the most unknown biomes concerning the plant below-ground system. Root biomass might be influenced by the availability of limiting resources and by the type and intensity of disturbances, mediated by the plant functional attributes related to environmental conditions. Fine and coarse roots should be affected differently: the former should be more responsive to resource supplies, whilst the latter should be related to changes in disturbance frequency. We studied the roles of soil fertility, topography of the plots indicating water availability, fire frequency and plant resistance to fire in affecting fine and coarse root biomass. We sampled the root biomass, environmental variables and functional attributes of all individuals present in 100 plots in savanna physiognomies of cerrado, in central Brazil. We used structural equation modelling to test our hypothesis and found that shallow root biomass, from 0 to 20 cm deep, was not caused by resource availability, by disturbances, as fire or drought, or by functional attributes. Biotic interactions were not considered in our study, but they may have a central role in affecting the shallow root biomass. In the deep layer, from 20 to 100 cm deep, we identified soil fertility and recent fires as the main factors causing changes in fine and coarse root biomass in the cerrado, respectively. Low nutrient availability in the soil caused higher fine root biomass, increasing the uptake of resources, whereas recent fires led to less coarse root biomass below 20 cm deep, probably due to the higher dominance of the herbaceous layer in the plots, with less coarse root biomass. According to our expectation, fine roots were mostly affected by nutrient availability in the soil, whereas coarse roots were more related to disturbance, in our case, recent fires.

**Key words:** fertility, fire, functional attributes, structural equation, topography.

## INTRODUCTION

In savannas, even though roots account for nearly 40% of the total plant biomass, the main drivers of below-ground biomass allocation are still largely unknown (Mokany *et al.* 2006). Root biomass might be influenced by the availability of limiting resources and by the type and intensity of disturbances affecting the communities, regulated by functional attributes of plant species (De Deyn *et al.* 2008; February *et al.* 2013). Considering that plants further divide biomass allocation between fine and coarse roots, the impacts of environmental drivers on root biomass are especially unclear (February *et al.* 2013). Plants likely respond to interplay between resource availability and disturbance intensity to regulate the amount of resources dedicated to fine and coarse root production (De Deyn *et al.* 2008; February *et al.* 2013).

Fine and coarse root biomass control resource uptake and contribute to survival after disturbance. Fine roots, up to 2 mm wide, are most responsible for

water and nutrient uptake, and should respond to their availability in the soil (Jackson *et al.* 1997; Forde & Lorenzo 2001). Compared with coarse roots, they are faster to produce and have higher turnover rate, being responsible for most of the carbon uptake in tropical areas (Gill & Jackson 2000). Coarse roots are costlier to produce, but have greater transport capacity, are less vulnerable to physical damage and are longer lived than fine roots (Fitter 1987). Coarse roots also have a structural role, working as resource storage organs some species use to re-sprout after disturbances (Coutinho 1990; Pausas & Keeley 2009). For these reasons, fine and coarse root biomass should be affected differently by nutrient availability and disturbance intensity: the former should be more responsive to the amount of resources in the soil, whilst the latter should be more related to changes in disturbance frequency, regulated by defensive functional attributes (Lei *et al.* 2012; Pärtel *et al.* 2012).

In the Brazilian cerrado, soil fertility is usually low (Gottsberger & Silberbauer-Gottsberger 2006), which limits plant biomass (Tilman *et al.* 1997; Forde & Lorenzo 2001). Fine root biomass tends to be higher in nutrient-rich zones and to decrease as nutrients

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become scarcer (Cleveland & Townsend 2006; Price *et al.* 2012). Nutrient availability is positively related to fine root ramification, length and biomass in grasses and herbs, but it shows no effect on coarse root biomass (Whiting *et al.* 2000; Lei *et al.* 2012). Moreover, in acidic soils, aluminium is solubilized and limits plant growth, reducing fine root biomass (Delhaize & Ryan 1995). In this sense, we expected root biomass to respond to surrogates of soil fertility: nitrogen and phosphorus availability, cation exchange capacity and aluminium content. On the one hand, fine root biomass should increase in soils with higher nitrogen and phosphorus availability, higher cation exchange capacity and lower aluminium content. On the other hand, coarse root biomass should not respond to these surrogates of soil fertility.

Among the disturbances that might affect biomass accumulation in cerrado communities, the most important are drought and fire (Gottsberger & Silberbauer-Gottsberger 2006). Drought can be more limiting than nutrient deficiency in the soil, limiting above- and below-ground plant growth (Ladwig *et al.* 2012). Some of the cerrado tree species produce deep roots to reach the groundwater, allowing tree growth and survival during the dry season (Oliveira *et al.* 2005). Also, shallow-rooted trees and grasses that do not reach the groundwater may be benefited by hydraulic lift promoted by their deep-rooted neighbours (Jackson *et al.* 1999). In this sense, deep root systems may help plant communities to overcome the limitation caused by drought. In the cerrado, topography affects water availability, changing the depth of the groundwater and the soil volume available for root growth (Oliveira-Filho & Ratter 2002; Rossatto *et al.* 2012). Deep groundwater and larger soil volumes are found in high altitudes and flat terrains (Rossatto *et al.* 2012). So we expected topographic variables, specifically high altitude and low slope, to be related with higher deep coarse root biomass at the community level, increasing water uptake and diminishing the impact of drought on plant communities (Rossatto *et al.* 2012).

Fire is another important disturbance in savanna communities, in a long history that has lasted nearly 20 million years, affecting both above- and below-ground plant biomass (Bond *et al.* 2005). Fire frequency is increasing in the last decades due to human activities, therefore it is important to predict how plant communities and the carbon pool will respond in this new scenario (Pausas & Keeley 2009). Fire consumes above-ground biomass and postpones the peak of fine root growth (Grime 1979; Di Iorio *et al.* 2011). A common strategy to survive frequent burning is to re-sprout after fire, using carbohydrates stored in the root system, usually in coarse roots (Pausas & Keeley 2009). Species able to re-sprout should be common in fire-prone communities, and their below-ground

systems are expected to be deeper and coarser than in communities protected from fire (Verdaguer & Ojeda 2002; Paula & Pausas 2011). Additionally, fire might have an indirect effect on root biomass by increasing soil fertility via nutrients deposited as ashes (Coutinho 1990; Silva & Batalha 2008).

In fire-prone communities, plants can have attributes that promote fire resistance, diminishing the damaging effects of fire on plants, such as the ability to re-sprout from the root system and thick bark to protect the inner living tissues (Pausas *et al.* 2004). Less-resistant plants should be more strongly impacted by fire, delay their biomass reconstruction, above- and below-ground (Zwicke *et al.* 2013). Some functional attributes are related to the root biomass in cerrado communities and they might help the understanding of the complex effect of the environment on the below-ground carbon pool (Loiola *et al.* 2015). Larger values of height, basal area and bark thickness increase plant resistance to fire, diminishing the damage and allowing a faster recovery after fire (Gignoux *et al.* 1997). Height and basal area change resistance to surface fires, the most common type of fire in the cerrado (Gottsberger & Silberbauer-Gottsberger 2006). Taller and thicker plants preserve their leaves from fire and are better protected from high temperatures during burnings (Bond *et al.* 2012). Thick barks insulate the inside living tissues against high temperatures and prevent death of above-ground organs (Hoffmann *et al.* 2009). We expected that functional attributes would regulate the effect of fire on the biomass and that fire-resistant plants should be less damaged by fire and have higher coarse root biomass.

Our goal was to test whether soil fertility (assessed through cation and aluminium availability), water availability (assessed through topographic variables), fire frequency and plant resistance to fire (assessed through height, basal area and bark thickness) would change fine and coarse root biomass in the cerrado. We tested these relationships for shallow and deep root biomass, as the distribution of nutrients, water and roots within the soil profile is not uniform. We expected that higher soil fertility, higher water availability, lower fire frequency and higher plant resistance to fire would increase root biomass, with different effects on fine and coarse root biomass. Fine roots should be more affected by resource availability, whilst coarse roots should be mostly affected by disturbances, drought and fire, regulated by plant resistance to fire.

## METHODS

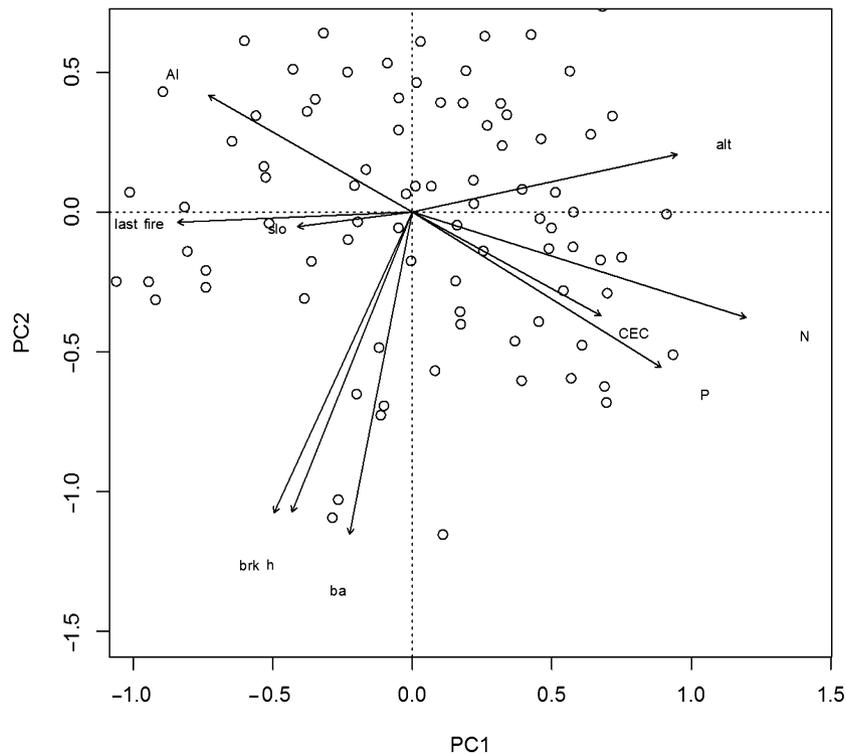
We carried out this study in Emas National Park (17°49'–18°28' S and 52°39'–53°10' W), central Brazil. With an area

of 132 941 ha, the park is among the most important cerrado reserves. The climate in Emas is Aw (Köppen 1931), with rainy summers and dry winters. The park lies within the Cerrado domain, mostly covered by savanna physiognomies of the cerrado vegetation. We placed 100 5 m × 5 m plots in the savanna, following a stratified random sampling design (Krebs 1998) with 10 strata of fire frequency, from the absence of fire to annual fire from 1984 to 2010, when we started the data sampling. In each plot, we sampled the root biomass to a depth of 100 cm. We extracted two soil monoliths of 40 cm × 40 cm × 20 cm, down to 40 cm deep. From 40 to 100 cm deep, we extracted a core using a 30 cm diameter auger (Castro & Kauffman 1998; Loiola *et al.* 2015). We separated the root sample in two layers, shallow and deep, the shallow layer comprising the first 20 cm of soil and the deep layer lying from 20 to 100 cm deep (Castro & Kauffman 1998). We sieved the soil with a 2-mm mesh and carefully washed the roots to eliminate adherent soil particles. We oven-dried the root samples at 70°C for 48 h and weighed them (Loiola *et al.* 2015).

We collected soil samples in each plot and assessed nitrogen, phosphorus, cation exchange capacity and aluminium content (Raij *et al.* 1987). We used nitrogen, phosphorus and cation exchange capacity as surrogates for soil fertility. As indicators of water availability to plants, we used topographic variables, measuring altitude and slope of each plot using an altimeter and an inclinometer. High altitudes and flat terrain are related to deep groundwater and should support larger

soil volume available to root growth (Rossatto *et al.* 2012). We considered the years elapsed since the last fire that occurred in each plot as a measure of fire frequency. Also, we identified all woody individuals with stem diameter at soil level equal to or larger than 3 cm and sampled three functional attributes as surrogates of fire resistance: basal area (m<sup>2</sup>), tree height (m) and bark thickness (mm). Each value was the average of that attribute for all individuals in a plot. The state of these attributes represents the plastic response of plant species to fire, and values should differ among fire regimes (Carvalho & Batalha 2013). We expected that higher values of height, basal area and bark thickness should provide better fire resistance to plants (Hoffmann *et al.* 2009; Bond *et al.* 2012).

We used a principal component analysis to present the environmental parameters among the plots and check for their covariation (Fig. 1). A general linear regression with the environmental variables was applied to the entire root biomass, without separating it into fine and coarse or shallow and deep roots. Even if the models were significant, they showed low explanatory power (Loiola *et al.* 2015). Therefore, in this study, we used structural equation modelling to test a model connecting soil fertility, topographic variables, fire frequency and plant resistance to fine and coarse root biomass. We proposed one *a priori* model (Fig. 2) and tested it on fine and coarse roots biomass in two different depths: shallow (0 to 20 cm) and deep (20 to 100 cm), using the 'lavaan' package (Rosseeel 2012) for R (R Core Team 2013).

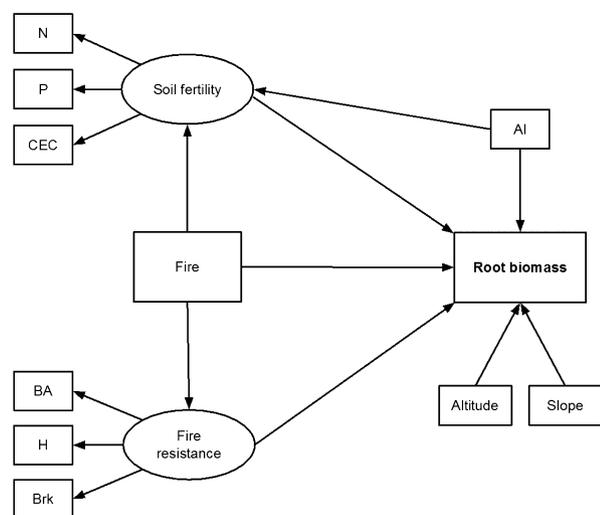


**Fig. 1.** Biplot of the principal component analysis (PCA) between the environmental variables and functional attributes along 100 plots in Emas National Park. Among topographic variables, alt (m) for altitude and slo (°) for slope; among soil variables, N (mg kg<sup>-1</sup>) for nitrogen content, CEC (mmol kg<sup>-1</sup>) for cation exchange capacity, P (mg kg<sup>-1</sup>) for phosphorus content and Al (mmol kg<sup>-1</sup>) for aluminium content; among functional attributes measured at individual level, ba (m<sup>2</sup>) for basal area, h for height (m), brk (mm) for bark thickness and fire for the years elapsed since the last fire that occurred in the plots before root sampling.

We did a confirmatory factor analysis with the variables that cause the latent variables (Carvalho & Batalha 2013). We used maximum likelihood estimation to estimate the parameters and assess the fit of the structural equation model. We used a robust estimator of standard errors to account for deviations from multivariate normality in our data.

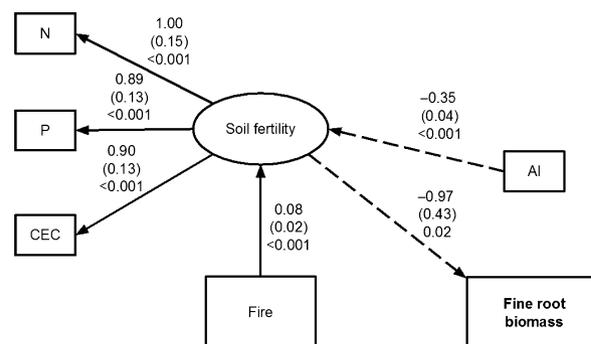
**RESULTS**

We present the mean and standard deviation of environmental variables and functional attributes meas-



**Fig. 2.** *A priori* casual model relating soil fertility, topographic variables, recent fire and plant resistance to fine and coarse root biomass in cerrado. We considered soil fertility a latent variable causing nitrogen (N, mg kg<sup>-1</sup>) and phosphorus (P, mg kg<sup>-1</sup>) content, and cation exchange capacity (CEC, mmol kg<sup>-1</sup>); plant resistance to fire causing basal area (BA, m<sup>2</sup>), height (H, m) and bark thickness (Brk, mm). Recent fire is the last fire that occurred in the plots before root sampling. This model was used four times, to fine and coarse root biomass (2 mm criteria) and to shallow and deep root biomass (20 cm deep criteria).

ured in each plot (Table 1). Also, the graph of a principal component analysis shows how the environmental variables and functional attributes vary among the plots (Fig. 1). The structural equation models for shallow root biomass exhibited a poor fit with the data, for both fine and coarse root biomass ( $P < 0.001$ , figures not shown). The model for deep fine root biomass fitted the data marginally ( $\chi^2 = 50.58$ , d.f. = 35,  $P = 0.04$ , Fig. 3). The model for deep coarse root fitted the data well ( $\chi^2 = 44.71$ , d.f. = 35,  $P = 0.12$ , Fig. 4). The latent variables exhibited strong fit with the data, and all variables showed significant path coefficients. The paths connecting aluminium content, topographic variables and fire resistance to root biomass were non-significant in all cases ( $P > 0.05$ ). Aluminium content had a negative effect on soil fertility in both cases, as we expected (coefficient = 0.04,  $P < 0.001$  for both deep fine and coarse root models). Also, soil fertility was positively affected by recent fire

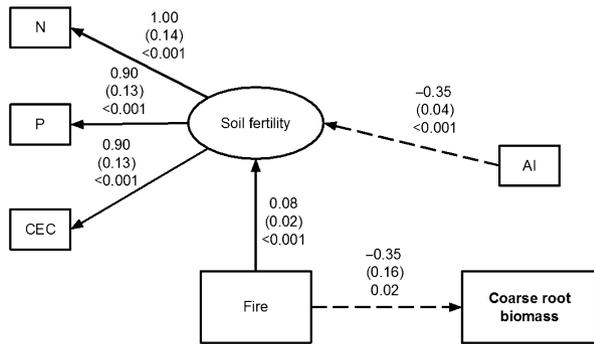


**Fig. 3.** Final model predicting deep fine root biomass, the root biomass sampled from 20 to 100 cm deep in the soil that had less than 2 mm diameter ( $\chi^2 = 50.58$ , d.f. = 35,  $P = 0.04$ ). Unstandardized estimates, standardized estimates between parenthesis and  $P$  values of each relationship, respectively, are presented for each line connecting the variables. Solid arrows indicate positive paths; dashed arrows indicate negative paths; non-significant paths were omitted.

**Table 1.** Mean and standard deviations of the variables used in the structural equation model causing fine and coarse root biomass

Resource availability		Disturbances		Functional attributes	
Variable	Mean ± SD	Variable	Mean ± SD	Variable	Mean ± SD
N	2013.1 ± 329.6	Altitude	797.6 ± 40.1	Height	1.61 ± 0.8
P	6.5 ± 1.7	Slope	2.1 ± 1.4	Basal area	0.003 ± 0.002
CEC	108.5 ± 34.5	Recent fire	5.1 ± 4.1	Bark thickness	10.1 ± 4.4
Al	18.4 ± 4.5				

Resource availability comprises soil variables sampled for each plot: N is nitrogen availability (mg kg<sup>-1</sup>), P is phosphorus availability (mg kg<sup>-1</sup>), CEC is cation exchange capacity (mmolc kg<sup>-1</sup>) and Al is for aluminium content (mmolc kg<sup>-1</sup>); among the disturbances, we included topographic variables indicating water availability of each plot: altitude (m) and slope (°); recent fire is the time elapsed in years since the last fire occurrence; resistance to fire, assessed through height (m), basal area (m<sup>2</sup>) and bark thickness (mm), was measured at individual level.



**Fig. 4.** Final model predicting deep coarse root biomass, the root biomass sampled from 20 to 100 cm deep in the soil that had more than 2 mm diameter ( $\chi^2 = 44.71$ , d.f. = 35,  $P = 0.12$ ). Unstandardized estimates, standardized estimates between parenthesis and  $P$  values of each relationship, respectively, are presented for each path connecting the variables. Solid arrows indicate positive paths; dashed arrows indicate negative paths; non-significant paths were omitted.

in both models (coefficient = 0.02,  $P < 0.001$  for both deep fine and coarse root models). Soil fertility had a negative effect on fine root biomass (coefficient = 0.43,  $P = 0.02$ ) and no effect on coarse root biomass (coefficient = 0.70,  $P = 0.92$ ). Recent fire had no effect on fine root biomass (coefficient = 0.09,  $P = 0.68$ ), but influenced negatively deep coarse root biomass (coefficient = 0.16,  $P = 0.02$ ). Plant resistance to fire was not related to recent fire in any case (coefficient = 0.10,  $P = 0.26$  for the deep fine root model; and coefficient = 0.18,  $P = 0.98$  for the deep coarse root model).

**DISCUSSION**

Among variables analysed, soil fertility was the only one affecting fine root biomass below 20 cm deep. Contrary to our expectation, however, soil fertility decreased fine root biomass of cerrado species (Forde & Lorenzo 2001). Fine roots are responsible for cation uptake from the soil and, thus, larger biomass of fine roots should increase the cation uptake (Forde & Lorenzo 2001). Even though most studies report higher fine root biomass in richer soil patches (Robinson 1994; Price *et al.* 2012), different responses might be given for the same environmental stimulus (Forde & Lorenzo 2001). In agreement with our results, fine root biomass production also decreased towards high nitrogen availability in a deciduous forest (Tateno *et al.* 2004). In nutrient-limited sites, such as the cerrado, abiotic filters may select species with attributes that allow them to overcome the limitations imposed by the environment (Keddy 1992; Tateno *et al.* 2004), such as increasing fine root biomass in low soil fertility sites.

Additionally, soil fertility was caused by differences in recent fires and aluminium content. Recent fires caused higher soil fertility, as we expected. The same result was found in African savannas, with recent fires increasing cation availability (Jensen *et al.* 2001). Even though parts of the chemicals and particles that compose the plant biomass are lost in the smoke by volatilization, part of the nutrients is deposited in the soil as ashes, increasing the cation availability (Coutinho 1990). Furthermore, plants lose young leaves after fires and litter with high nutrient content accumulates on the soil, leading to higher soil fertility (Rodríguez *et al.* 2009). Besides recent fires, high aluminium content caused low soil fertility, indirectly affecting the root biomass. Aluminium is related to acidic soils, to low concentration of nutrients and is more abundant in communities with low density of woody individuals. We found no evidence of aluminium causing a decrease in root biomass, as suggested by the literature (Goodland & Pollard 1973; Fierer & Jackson 2006). However, the variability of plant species to aluminium may allow them to resist the toxicity affecting root growth (Kochian 1995). We suggest that plant resistance to high aluminium content in soil may be a common strategy in cerrado communities.

Also, differences in topographic variables indicating water availability did not affect fine or coarse root biomass in the cerrado. We expected that deep groundwater, found in high altitudes and flat terrains, would increase the soil volume available to the root system, increasing root growth and water uptake (Rossatto *et al.* 2012; Loiola *et al.* 2015). In Emas, water availability is a determinant of the vegetation structure, increasing the functional diversity of the plots (Carvalho *et al.* 2014). When we analysed the entire root system, considering both fine and coarse roots, we found that the altitude of the plots was related to root biomass (Loiola *et al.* 2015). However, this relationship could not be observed when we sorted root biomass into fine and coarse roots in two different depths. Even though water availability seems to affect the below-ground carbon pool, the effect was only revealed when we accounted for the cumulative effect on fine and coarse root biomass.

In contrast to water availability, the effect of fire on root biomass could only be observed when we separated fine and coarse roots. Contrary to what we expected, recent fires decreased coarse root biomass. Even though fire is expected to stimulate below-ground storage in coarse root organs, it might favour grasses instead of trees, with less coarse root biomass (Bond & Keeley 2005; February *et al.* 2013). As we expected, fire had no effect on fine root biomass below 20 cm deep. The effect of disturbances on fine root biomass, such as drought and fire, may be missed because fine roots have high turnover in tropical sites (Gill & Jackson 2000). The replacement of lost fine

roots can happen shortly after the disturbance and leave no trace on the fine root biomass after 1 year (Pärtel *et al.* 2012).

Plant resistance to fire, assessed through functional attributes, did not affect fine or coarse root biomass and was also not related to recent fires. Fire does not seem to act as an environmental filter leaving a signal in functional attributes in cerrado communities (Loiola *et al.* 2010; Carvalho *et al.* 2014). Our results give support to the insurance theory, which states that species composition might change in sites subjected to different frequencies of environmental filters without losing functional diversity or affecting community processes (Yachi & Loreau 1999; Loreau & Hector 2001). Other studies in cerrado also showed that fire is not related to different functional diversity of communities, even though it is related to differences in above-ground biomass and species (Cianciaruso *et al.* 2010, 2012; Carvalho *et al.* 2014). In the cerrado, plant species seem to be selected by fire at the regional scale, and changes in local fire frequency do not imprint differences in functional strategies.

Shallow root biomass, in the top 20 cm of the soil, is a large portion of the carbon pool, near 80% of the root biomass (Jackson *et al.* 1996). Contrary to our expectation, shallow root biomass in cerrado was not caused by resource availability or by disturbances, such as fire or drought. Even though abiotic factors are expected to be determinants of below-ground biomass production (Price *et al.* 2012), the most important abiotic filters of cerrado did not cause differences in the shallow root biomass. Biotic interactions were not considered in our study, but they may impact shallow root biomass. Competition and facilitation can change species similarity and impact community properties, especially under nutrition-limited sites (Stubbs & Wilson 2004). Moreover, the herbaceous layer contributes to a high amount of biomass and cover in the cerrado, affecting fire dynamics, nutrient distribution and decomposition rates (França *et al.* 2007; Carvalho *et al.* 2014). The herbaceous species composition and their functional resistance to fire might explain the shallow root biomass investment in cerrado.

Understanding how resource availability and disturbance interact and lead to changes in the community functioning might be critical for conservation of diversity, properties and processes in natural communities (Srivastava & Vellend 2005; Grace *et al.* 2007). Many aspects of the environment may be interconnected through different paths and affect the carbon pool and cycling (Diaz *et al.* 2007). Using structural equation modelling, we were able to identify soil fertility and recent fires as the main environmental factors causing changes, respectively, in deep fine and coarse root biomass in the cerrado. Plant response to the lack of nutrients in the soil increases fine root biomass and consequently the uptake of limiting resources, whereas

recent fires lead to less coarse root biomass below 20 cm deep, probably due to the higher dominance of the herbaceous layer in these plots. According to our expectation, fine roots were mostly affected by nutrient availability in the soil, whereas coarse roots were more related to disturbance, in our case, recent fires.

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