UNIVERSIDADE FEDERAL DE SÃO CARLOS

Programa de Pós-Graduação em Ecologia e Recursos Naturais

PRISCILLA DE PAULA LOIOLA

Biomassa e produtividade subterrânea no cerrado: relações com solo, topografia e fogo

São Carlos

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Tese apresentada ao Programa de Ecologia e Recursos Naturais, do Centro de Ciências Biológicas e Saúde, para a obtenção do título de doutor.

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Sumário

ABSTRACT

Plant biomass and productivity are ecological properties that affect community functioning. The belowground biomass of cerrado is underestimated and, therefore, it is important that we know how it is related to biotic and abiotic variables. In the first chapter, we tested for the relationship between different diversity indices and above- and belowground biomass. Species diversity and functional divergence positively affected the aboveground biomass, but not the belowground biomass, both in the cerrado and in the seasonal forest. Resource use complementarity led to a better community functioning, but did not predict all the community biomass production, as it disregarded the belowground component. Inclusion of environmental variables and functional traits, in the second chapter, was important to generate models that predicted the belowground biomass. The models were significant, even tough they showed low explanatory power for the cerrado. Foraging for limiting nutrients, altitude, and functional traits related to disturbance were selected in the models predicting the belowground biomass. In the third chapter, we separated fine and coarse roots in two depths. We used structural equation modeling to test for the effects of environmental variables on the belowground biomass in each root category and each depth. We identified soil fertility causing less fine root biomass and recent fire causing less coarse root in the deep soil layer. Shallow root biomass was not caused by any of the ecological processes we studied. Also, aluminum content led to low soil fertility and recent fire caused higher soil fertility, as we expected. The carbon stock of the cerrado and the seasonal forest is large and should not be neglected when estimating the impacts caused by climate and land-use changes.

Keywords: carbon, functional diversity, ingrowth core, root, tropical seasonal forest

RESUMO

A biomassa e a produtividade das plantas são propriedades ecológicas importantes para o funcionamento das comunidades. A biomassa hipógea do cerrado é subestimada, por isso, é importante sabermos sua dimensão e como ela se relaciona com fatores bióticos e abióticos. No primeiro capítulo, testamos a relação entre índices de diversidade e as biomassas epígea e hipógea. A diversidade de espécies e a divergência funcional estiveram relacionadas com a biomassa epígea, mas não com a biomassa hipógea, tanto no cerrado quanto na floresta estacional. A complementaridade no uso dos recursos levou a um melhor funcionamento das comunidades, mas não explicou toda a produção de biomassa vegetal. A inclusão de variáveis ambientais e traços funcionais, no segundo capítulo, gerou modelos que explicaram a alocação da biomassa e produtividade hipógeas. Os modelos foram significativos, apesar de terem baixo poder preditivo no cerrado. O forrageamento por nutrientes, a altitude e os traços funcionais relacionados aos distúrbios foram selecionados nos modelos prevendo a biomassa hipógea. No terceiro capítulo, separamos as raízes em finas e grossas e em dois estratos de profundidade. Usamos modelos de equações estruturais para testar os efeitos das variáveis ambientais na biomassa das raízes de cada estrato. Identificamos a fertilidade do solo causando menor biomassa de raízes finas e fogos recentes levando a menor biomassa de raízes grossas profundas. A biomassa das raízes superficiais não foi causada por nenhum dos processos ecológicos estudados e deve estar relacionada a interações bióticas. Há também relação entre a quantidade de alumínio e menor fertilidade do solo, e fogos recentes causaram maior fertilidade do solo. O estoque de carbono no cerrado e na floresta estacional semidecidual são grandes e não devem ser ignorados quando estimamos o impacto causado por mudanças climáticas e no uso da terra.

Palavras-chave: anéis de crescimento, carbono, diversidade funcional, floresta estacional semidecidual, raízes

I - INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

A biomassa acumulada e a produtividade anual das plantas, ou seja, a produção de tecido vegetal que sustenta toda a cadeia alimentar, são propriedades ecológicas importantes para os ciclos biogeoquímicos e para o funcionamento das comunidades (Tilman et al. 2001). Diferenças na quantidade de biomassa das plantas representam mudanças no estoque de carbono das comunidades, determinando se elas funcionarão como fonte ou sumidouro de dióxido de carbono (Fearnside 2000, Tilman et al. 2001). Se as áreas protegidas forem convertidas para uso antrópico, o carbono acumulado nos tecidos vegetais será emitido para a atmosfera, aumentando os efeitos do aquecimento global e a velocidade das mudanças climáticas (Castro & Kauffman 1998). Portanto, é importante que tenhamos medidas precisas da quantidade e da produtividade anual de biomassa das comunidades vegetais, e como essas medidas estão relacionadas a fatores bióticos e abióticos, para prevermos os impactos no estoque de carbono causados pelas atuais mudanças ambientais (Fearnside & Laurance 2004).

A biomassa epígea das árvores é bem estudada e existe uma variedade de estimativas que podemos usar para prever a quantidade de carbono estocada acima do solo nas comunidades (Chave et al. 2005, Delitti et al. 2006). Na porção subterrânea, no entanto, as medidas de biomassa e produtividade são difíceis de serem obtidas, dificultando a avaliação do papel das comunidades vegetais no ciclo do carbono (Johnson & Matchett 2001). A base de dados de biomassa de raízes e o tamanho do estoque de carbono no subsolo permanece impreciso e é, provavelmente, subestimado (Robinson 2007). Em muitos trabalhos, o número de parcelas usado para estimar a biomassa subterrânea é pequeno ou os métodos não são bem detalhados, fazendo com que o levantamento de dados seja inadequado ou inverificável (Mokany et al. 2006). A quantidade e a produtividade da biomassa vegetal subterrânea devem ser mais acuradas para que sejam consideradas na modelagem global do carbono (Hui &

Jackson 2006).

No cerrado, a subestimativa da biomassa subterrânea é ainda mais evidente, uma vez que algumas espécies apresentam raízes mais profundas se comparadas às de plantas de outras vegetações (Canadell et al. 1996). O cerrado ficou conhecido nas palavras do escritor Carmo Bernardes como 'floresta de cabeça para baixo', porque sua biomassa hipógea é maior do que a biomassa epígea (Abdala et al. 1998). Algumas espécies vegetais do cerrado têm raízes que permitem o acesso à água estocada profundamente no solo, importantes para a sobrevivência durante a estação seca (Meinzer et al. 1999, Oliveira et al. 2005). Além disso, as raízes das plantas de cerrado podem funcionar como estratégia de resistência às altas frequências de fogo (Pausas & Keeley 2009). Órgãos e estruturas subterrâneos, como bulbos, rizomas, e xilopódios, ficam protegidos das altas temperaturas, e armazenam carboidratos e nutrientes usados após a queimada para reconstruir a biomassa epígea consumida pelo fogo (Coutinho 1990). Por isso, a vegetação do cerrado tem uma importante biomassa subterrânea, relativamente maior do que a de outras vegetações.

Um dos fatores que pode influenciar a biomassa das comunidades vegetais é a diversidade das espécies que as compõem (Tilman et al. 1997, Ruiz-Jaen & Potvin 2010). Comunidades mais diversas podem conter espécies complementares no uso dos recursos e devem ter um melhor funcionamento e maior produção de biomassa (Tilman et al. 1997, Cardinale et al. 2006). A alta diversidade de espécies reduz a variação na produtividade de biomassa ao longo do tempo, promovendo um efeito de tamponamento e aumentando o desempenho geral (Yachi & Loreau 1999). No entanto, a maior parte dos trabalhos que testaram a relação entre diversidade de espécies e biomassa foram desenvolvidos em florestas ou campos temperados, em casas de vegetação ou em experimentos com diversidade controlada (Balvanera et al. 2006). Os altos valores nos índices de diversidade de espécies nem sempre resultam em aumento na biomassa das comunidades, e esse efeito foi menos frequentemente testado em comunidades naturais tropicais (Balvanera et al. 2006). O efeito e a força dessa relação dependem da diversidade inicial, do desenho experimental e do distúrbio que afeta a área estudada (Balvanera et al. 2006).

As diferenças interespecíficas no requerimento de recursos mudam a amplitude do efeito da diversidade na produtividade da comunidade (Tilman et al. 1997). Dado que as espécies não têm efeitos iguais sobre o funcionamento das comunidades, é importante levar em consideração os traços funcionais das espécies (Loreau 1998, Mouchet et al. 2010). Espécies funcionalmente distintas, ou seja, com traços funcionais diferentes entre si, devem usar diferentes espectros dos recursos e afetar o funcionamento da comunidade (Petchey & Gaston 2006). Dessa forma, maiores índices de diversidade funcional devem afetar os processos e propriedades ecológicas, aumentando, por exemplo, a biomassa e produtividade das plantas (Díaz & Cabido 2001). Assim, no primeiro capítulo desta tese, testamos se o aumento da diversidade de espécies e da diversidade funcional leva a um aumento das biomassas epígea e hipógea e da produtividade anual de raízes finas em comunidades de cerrado.

Além de estar relacionada a medidas de diversidade, a produção de biomassa das plantas está relacionada à imprevisibilidade e à complexidade ambientais (Fridley 2001). A fertilidade do solo, por exemplo, é um fator que afeta a produtividade da biomassa das plantas. Raízes finas, com menos de 2 mm de diâmetro, são as principais responsáveis pela absorção de nutrientes e água do solo, recursos muito importantes para as espécies de plantas do cerrado (Oliveira et al. 2005). Se os nutrientes e a água são limitados, a comunidade pode investir em alta produção de biomassa hipógea, aumentando a captação dos recursos (Tateno et al. 2004). De acordo com outros trabalhos, no entanto, solos mais ricos em nutrientes podem apresentar alta produtividade de biomassa de raízes (Casper & Jackson 1997, Fridley 2002). Logo, a disponibilidade de recursos, como nutrientes e água disponíveis no solo devem alterar a produção de raízes das espécies de cerrado.

Outro fator ambiental particularmente importante é o fogo, um processo importante na composição e distribuição das comunidades (Bond et al. 2005). As savanas, como o são a maior parte das fisionomias de cerrado, convivem com o fogo por pelo menos 20 milhões de anos (Bond et al. 2003). O fogo altera a estrutura da vegetação savânica e a eficiência no uso dos nutrientes do solo (Bond et al. 2005). Além disso, os regimes de fogo mudam os tipos funcionais presentes nas comunidades, de arbustos e árvores com raízes profundas para gramíneas com raízes superficiais, alterando a estabilidade dos estoques de água e diminuindo o estoque de carbono potencial (Pausas & Keeley 2009). O fogo associado com a expansão da agricultura afeta os reservatórios de carbono, liberando uma grande quantidade de carbono na combustão de árvores, arbustos e gramíneas (Mouillot & Field 2005, Pausas & Keeley 2009). Dessa forma, entender como a biomassa hipógea responde a diferentes frequências de fogo é essencial para entender a dinâmica do estoque de carbono no cerrado. Considerando a biomassa subterrânea, o fogo pode tanto aumentar o crescimento das raízes (Johnson & Matchett 2001), quanto diminuir a biomassa subterrânea em sítios queimados frequentemente (Delitti et al. 2001).

No segundo e no terceiro capítulos, incluímos variáveis ambientais, como qualidade nutricional do solo, variáveis topográficas como medidas de acesso à água nas parcelas, e frequência e última ocorrência de queimadas, para testar quais fatores influenciam a biomassa hipógea no cerrado. No segundo capítulo, buscamos construir modelos que melhor explicassem a alocação da biomassa hipógea e a produtividade anual de raízes finas tanto no bioma savânico quanto no florestal. No terceiro capítulo, separamos as raízes em finas e grossas, com o critério de 2 mm de diâmetro, e em estratos de profundidade, superficial e profundo, com o critério de 20 cm. Usamos modelos de equações estruturais para testarmos os efeitos das variáveis ambientais na alocação de biomassa das raízes em cada uma dessas frações.

Coletamos os dados usados nesta tese no Parque Nacional das Emas (PNE), Goiás. O PNE é uma importante reserva de cerrado no Brasil, com aproximadamente 133.000 ha. O PNE possui histórico detalhado de imagens de satélite das queimadas nos últimos 30 anos, o que permitiu que incorporássemos a variabilidade das frequências de fogo nas nossas análises (França et al. 2007). O parque foi criado em 1961, porém sua regularização fundiária só aconteceu em 1984, levando à exclusão da criação de gado no interior do parque e o início da política de prevenção do fogo (França et al. 2007). O PNE possui relevo suave e altitudes que variam de 800 a 900 m (França et al. 2007). Os solos são dos tipos latossolo vermelho-escuro distrófico e latossolo vermelho-amarelo distrófico. O clima no parque é estacional tropical, com temperatura média anual de 24,6°C e a pluviosidade anual está entre 1200 e 2000 mm, distribuídos heterogeneamente ao longo do ano (Ramos-Neto & Pivello 2000). Os meses mais secos são junho, julho e agosto, quando a precipitação é inferior a 60 mm (França et al. 2007). A vegetação no interior do parque vai desde o campo limpo, com o predomínio do componente herbáceo, até o cerrado sensu stricto, onde predomina o componente arbustivo-arbóreo. Há ainda áreas menores de campos úmidos, veredas de buritis e florestas estacionais semideciduais (França et al. 2007).

Amostramos a biomassa hipógea até a profundidade de 100 cm. Extraímos os primeiros 40 cm de solo com um monolito com 40 cm de lado, separados em dois horizontes de 20 cm de profundidade cada (Castro & Kauffman 1998). Para extrairmos os monolitos com precisão, fundimos uma barra de ferro a uma placa afiada também de ferro e usamos uma marreta para inserirmos a barra no solo, cortando as raízes (Figura 1). De 40 cm a 100 cm de profundidade, extraímos o solo usando uma perfuratriz movida a gasolina e uma broca com 30 cm de diâmetro (Castro & Kauffman 1998). Usamos uma peneira de 2 mm de diâmetro para separar as raízes do solo coletado. As raízes retidas na peneira foram levadas ao laboratório, onde foram lavadas em água corrente, colocadas na estufa a 70°C durante 48 h e pesadas.

Para amostrarmos a produtividade anual das raízes finas, instalamos anéis de crescimento circulares com 20 cm de diâmetro (Milchunas et al. 2005). No entanto, o método proposto por (Milchunas et al. 2005) instalava os anéis com a ajuda de um trator, procedimento pouco viável para ser aplicado em parques nacionais no Brasil. Dessa forma, instalamos os anéis com a ajuda de um cilindro afiado de ferro, reforçado com uma barra de suporte, que cortava o solo na medida exata dos anéis de crescimento (Figura 2).

De posse dos dados de biomassa total das raízes e produtividade anual das raízes finas, respondemos às seguintes perguntas: (i) comunidades com maior índice de diversidade de espécies ou maior diversidade funcional apresentam maior biomassa epígea e hipógea?; (ii) podemos prever a biomassa hipógea do cerrado e da floresta estacional semidecidual usando a qualidade nutricional do solo, variáveis topográficas, frequência de queimadas das parcelas e traços funcionais das espécies?; (iii) a disponibilidade de recursos no solo e os distúrbios afetam diferentemente a biomassa de raízes finas e grossas, em diferentes profundidades de solo?

Apresentamos a tese em forma de capítulos, que estão formatados de acordo com as normas das revistas científicas a que foram ou serão submetidos. Os artigos estão redigidos em inglês, de acordo com a exigência dos periódicos. O primeiro capítulo foi formatado para ser submetido ao periódico Oecologia; o segundo capítulo foi submetido ao periódico Forest Ecology and Management; o terceiro capítulo foi formatado para ser submetido ao periódico Austral Ecology.

Figura 1 - Placa de ferro e marreta usadas para cortar o monolito de solo com exatos 40 cm de lado. Após o corte do solo e das raízes, o monolito foi extraído e o solo, peneirado, para separarmos as raízes coletadas.

Figura 2 - Cilindro de ferro afiado na base, usado para a instalação dos anéis de crescimento de forma manual.

Referências

Abdala GC, Caldas LS, Haridasan M, Eiten G (1998) Above and belowground organic matter and root:shoot ratio in a cerrado in Central Brazil Braz J Ecol 2:11–23.

Balvanera P, Pfisterer AB, Buchmann N, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156.

Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Glob Change Biol 9:973–982.

Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. New Phytol 165:525–538.

Canadell J, Jackson RB, Ehleringer JR, et al. (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595.

Cardinale BJ, Srivastava DS, Emmett Duffy J, et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Casper BB, Jackson RB (1997) Plant competition underground. Ann Rev Ecol Syst 28:545–570.

Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. J Trop Ecol 14:263–283.

Chave J, Andalo C, Brown S, et al. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99.

Coutinho LM (1990) Fire in the ecology of the Brazilian cerrado. In: Goldammer JC (ed) Fire in the tropical biota. Springer, Berlin, pp. 81–103.

Delitti WBC, Meguro M, Pausas JG (2006) Biomass and mineralmass estimates in a “cerrado” ecosystem. Braz J Bot 29:531–540.

Delitti WBC, Pausas JG, Burger DM (2001) Belowground biomass seasonal variation in two Neotropical savannahs (Brazilian Cerrados) with different fire histories. Ann For Sci 58:713–721.

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655.

Fearnside PM (2000) Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. Climatic Change 46:115–158.

Fearnside PM, Laurance WF (2004) Tropical deforestation and greenhouse-gas emissions. Ecol App 14:982–986.

França H, Ramos-Neto MB, Setzer A (2007) O fogo no Parque Nacional das Emas. Ministério do Meio Ambiente. 141 p.

Fridley J (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. Oecologia 132:271–277.

Fridley JD (2001) The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93:514–526.

Hui D, Jackson RB (2006) Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data. New Phytol 169:85–93.

Johnson LC, Matchett JR (2001) Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389.

Loreau M (1998) Separating sampling and other effects in biodiversity experiments. Oikos 82:600–602.

Meinzer FC, Goldstein G, Franco AC, et al. (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. Funct Ecol 13:273–282.

Milchunas DG, Mosier AR, Morgan JA, et al. (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: using a new ingrowth method. Plant Soil 268:111–122.

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root : shoot ratios in terrestrial biomes. Glob Change Biol 12:84–96.

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876.

Mouillot F, Field CB (2005) Fire history and the global carbon budget: a fire history reconstruction for the 20th century. Glob Change Biol 11:398–420.

Oliveira RS, Bezerra L, Davidson EA, et al. (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. Funct Ecol 19:574–581.

Pausas JG, Keeley JE (2009) A burning story: the role of fire in the history of life. BioScience 59:593–601.

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758.

Ramos-Neto MB, Pivello VR (2000) Lightning fires in a Brazilian savanna national park:

rethinking management strategies. Environ Manag 26:675–684.

Robinson D (2007) Implications of a large global root biomass for carbon sink estimates and for soil carbon dynamics. P Natl Acad Sci 274:2753–2759.

Ruiz-Jaen MC, Potvin C (2010) Tree diversity explains variation in ecosystem function in a neotropical forest in Panama. Biotropica 42:638–646.

Tateno R, Hishi T, Takeda H (2004) Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. Forest Ecol Manag 193:297–306.

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. P Natl Acad Sci 94:1857–1861.

Tilman D, Reich PB, Knops J, et al. (2001) Diversity and productivity in a long-term grassland Exp Sci 294:843–845.

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. P Natl Acad Sci 96:1463–1468.

II - CAPÍTULO 1

Artigo formatado para ser submetido ao periódico Oecologia

The relationship between tree diversity and plant biomass and root productivity in savanna and tropical seasonal forest

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Abstract

High diversity should increase complementarity in resource use among species and increase biomass production in plant communities. We tested whether species diversity and functional diversity, depicted as functional richness, evenness, and divergence, were related to higher plant biomass and root productivity, and whether the relationships were similar above- and belowground in savanna and seasonal forest. We estimated the aboveground biomass and sampled the root biomass and productivity in 100 plots in savanna and 20 plots in seasonal forest, in Central Brazil. We used 12 functional traits to calculate the functional diversity indices and general linear regression models to test our hypothesis. Aboveground standing biomass could be partially predicted by both species diversity and functional divergence, but not by functional richness and functional evenness. However, differences in aboveground diversity indices were not related to root biomass or productivity. More efficient use of resources due to niche complementarity may be a mechanism affecting aboveground plant biomass, but to estimate belowground carbon pool, the inclusion of abiotic variables might be necessary.

Keywords: biomass, cerrado, divergence, evenness, richness

Introduction

Currently, the functional role of diversity affecting the community processes is being studied in depth, and diversity is expected to be a good estimator of plant biomass production (Sala et al. 2000; Cardinale et al. 2006). High diversity could allow a better use of limiting resources as a result of high complementarity among species and, therefore, be related to highly productive communities (Tilman et al. 1997; Cardinale et al. 2006). However, most studies on diversity affecting plant biomass production were conducted on grasslands or short-lived model systems, and only few in natural tropical areas where species diversity is high (Cardinale et al. 2011; Scherer-Lorenzen 2013). Moreover, because results on species diversity affecting community functioning are controversial regarding the initial diversity of the site studied, the experimental design, the type of disturbance, and the vegetation type analysed, there is no consensus on whether biodiversity influence plant biomass under natural communities (Balvanera et al. 2006). Strong effects of diversity on ecological properties were found under experimental conditions, such as greenhouses or field experiments, with rather homogeneous site conditions (Balvanera et al. 2006; Cardinale et al. 2011).

In tropical plantations, the link between the carbon pools and fluxes become stronger when the diversity is higher (Potvin et al. 2011). Studies in non-controlled, natural communities are less common and show a weaker effect of diversity on plant biomass when compared with controlled experiments (Balvanera et al. 2006; Scherer-Lorenzen 2013). If we take into account natural communities with high diversity indices, data on plant biomass, especially belowground, are not accurate (Mokany et al. 2006). Savannas and tropical forests are among the less understood communities concerning plant biomass, particularly root biomass, due to the lack of replicates and unverifiable sampling methods (Mokany et al. 2006). In Brazil, savannas and tropical seasonal forest occur within the Cerrado domain, a large area which originally occupied about 25% of the Brazilian territory and represents a major share of the global carbon pool (Ratter et al. 1997). With high richness and high degree of endemism, the Cerrado domain is considered one of the world's hotspots for biodiversity conservation (Myers et al. 2000). Nonetheless, only a small portion of the Cerrado is protected, about 2.2% of its total area, and the loss of plant biomass is a main problem for climate change mitigation (Marris 2005; Scherer-Lorenzen 2013)

To understand better the effects of biodiversity on biomass allocation pattern, we might consider not only traditional diversity measures based on taxonomic units but also functional diversity indices (Petchey et al. 2004; Hooper et al. 2005). High functional differences among species may positively affect ecological processes and properties, such as plant biomass and productivity (Díaz and Cabido 2001). High functional diversity leads to coexistence of species with different niche requirements and higher complementarity on the use of resources, and therefore to high productivity of plant communities (Tilman et al. 1997). For example, functional diversity impacts aboveground productivity and the decomposability of organic matter in grasslands (Klumpp and Soussana 2009). Functional diversity can be divided into primary components that might affect ecological processes (Mason et al. 2005). Each component describes an aspect of functional diversity, identifying niche filtering, limiting similarity, and neutral assembly (Mouchet et al. 2010) Thus, decomposing functional diversity might unravel its role on community functioning, and the influence of biotic interactions and abiotic filters on the structure of plant communities (Villéger et al. 2008).

A commonly used system distinguishes among functional richness, evenness, and divergence (Mason et al. 2005; Villéger et al. 2008). These different components vary independently and may affect plant biomass and productivity (de Bello et al. 2006; Mouchet et al. 2010). Functional richness represents the functional space filled by the community, and variations in this functional volume reflect changes driven by environmental pressure (Cornwell et al. 2006; Schleuter et al. 2010). Functional evenness describes the regularity with which the functional space is filled by species, weighted by their abundances, whereas functional divergence is related to how abundances are distributed within the volume of functional trait space occupied by species (Villéger et al. 2008).

Shifts in the distribution of species abundances within the functional space, assessed through functional evenness and functional divergence, result from shifts in the intensity of competitive interactions (Mason et al. 2007, 2008). Instead of using a general index of functional diversity, these functional components should be considered separately to clarify the relation of each aspect of functional diversity with community properties, as above- and belowground plant biomass (Schleuter et al. 2010)

In this study, we asked whether diversity predicts above- and belowground plant biomass, as well as root productivity, of savannas and tropical forests. Specifically, we tested whether higher Shannon index of species diversity and higher functional diversity, depicted as functional richness, evenness, and divergence, were related to higher plant biomass and root productivity, and whether the relationships had similar strength above- and belowground. We expected that because high diversity is related to high complementarity in resource use, that is, better use of limiting resources, high diversity should be associated with above- and belowground standing biomass and root productivity, both in the savanna and in the seasonal forest.

Methods

We carried out this study in Emas National Park, central Brazil, at 17°49’-18°28’S and 52°39’-53°10’W. The park has 132,941 ha (França et al. 2007) and an Aw climate of dry winters and rainy summers (Köppen 1931). Most of the park is covered by cerrado vegetation, prevailing savannas with different tree densities (França et al. 2007). Other vegetation types, such as riparian forest, semideciduous seasonal forest, and floodplain grassland, also occur. In the savanna, we placed 100 5 m x 5 m plots using a stratified random sampling design (Krebs 1998), comprising 10 categories of fire frequency. The fire categories went from absence of fire to annual fire in the last 16 years. In the semideciduous seasonal forest, as there was no variation in fire frequency, we established systematically 20 5 m x 5 m plots, separated 50 m from each other (see Dantas et al. 2013 for details).

On each plot, we identified all tree species with stem diameter at soil level equal to or larger than 3 cm. On each individual, we measured 12 performance and functional traits related to nutrition, growth, and resistance to disturbance: basal area, height, bark thickness, wood density, specific leaf area, leaf size, leaf toughness, leaf nitrogen content, leaf phosphorous content, and leaf potassium content (Pérez-Harguindeguy et al. 2013). We also included top kill as a functional trait, defined as stem mortality driven by fire, followed by resprouting from the root system (Hoffmann et al. 2009). Higher top kill rates should be related to lower aboveground biomass, which is directly consumed by the fire, and to higher belowground biomass, used to store carbohydrates and resprout after fire (Hoffmann et al. 2009; Paula and Pausas 2011). We also calculated tortuosity, the length:height ratio of the main branch up to the first bifurcation, indicative of fire resistance (Higgins et al. 2007). The straighter the tree, the safer it is from surface fires, the most common type of fire in the cerrado. So we expected low tortuosity to be related to higher plant biomass and root productivity (França et al. 2007).

We used species identities and abundances in each plot to calculate species diversity using the Shannon index (Magurran 2004) Moreover, we used functional traits to calculate functional richness (Petchey and Gaston 2006), functional evenness (Villéger et al. 2008), and functional divergence (Rao 1982) of each plot, following Schleuter et al. (2010). Functional evenness and divergence take into account the species abundances in the plots (Villéger et al. 2008).

We estimated the aboveground biomass of each plot summing up the biomass of all individuals within it. In the savanna, we used an allometric equation developed for cerrado trees (Delitti et al. 2006):

$AGB = 28.77 \times d^2 \times h$, in which *AGB* is the aboveground biomass (g), *d* is the diameter (cm) and *h* is the height of the tree (m).

In the seasonal forest, we estimated the aboveground biomass with an equation developed for dry tropical forests (Chave et al. 2005):

$\ln AGB = -2.68 + 1.805 \ln(d) + 1.038 \ln(h) + 0.377 \ln(w)$, in which *AGB* is the aboveground biomass (kg), *d* is diameter (cm), *h* is height (m), and *w* is wood density (g cm^{-3}) of the tree.

We sampled the total root biomass of each plot to the depth of 100 cm, which comprises more than 80% of the root biomass in savannas and tropical forests (Jackson et al. 1996; Castro and Kauffman 1998). We extracted the soil in the upper 40 cm of soil with a monolith of 40 cm width (Castro and Kauffman 1998). Then, we used an auger of 30 cm diameter to extract the soil from 40 to 100 cm deep (Castro and Kauffman 1998). We sieved all soil sampled using a 2 mm mesh to separate the roots and we eliminated the remaining soil particles washing the roots individually. We dried the root samples in the oven at 70°C for 48 hours to constant mass and weighted them. We assessed fine root productivity, those roots with less than 2 mm diameter, with an ingrowth core method (Milchunas et al. 2005). The cores had 20 cm diameter, 40 cm deep, and an area of 2.5 cm wide used to grow the roots (Milchunas et al. 2005). We placed the cores before the rainy season and measured the root biomass produced inside the core after one year.

We used a general linear regression model to test whether diversity indices were positively related to above- and belowground biomass and root productivity. As explanatory variables, we used the Shannon index, functional richness, functional evenness, and functional divergence. To avoid circularity, we excluded from the analysis of the functional diversity indices used to be related to the aboveground biomass, the traits used to estimate the aboveground biomass– diameter, height, and wood density. We used all traits to calculate the functional indices used to predict the belowground biomass. Data were log-transformed when necessary to reach normality in the residuals. We did all analyses in R using the 'stats' package (R Development Core Team 2012).

Results

In the 100 savanna plots, we sampled 531 individuals belonging to 55 species and, in the 20 forest plots, we sampled 185 individuals belonging to 43 species. Estimated aboveground biomass was 20.15 ± 16.26 Mg ha^{-1} for the savanna and 125.84 ± 122.22 Mg ha^{-1} for the seasonal forest (mean ± standard deviation). Root biomass to one-meter deep in the savanna was 29.78 ± 21.74 Mg ha^{-1} and 38.33 ± 28.37 Mg ha^{-1} in the seasonal forest. Fine root productivity was 98.9 ± 41.55 g m^{-2} year^{-1} in the savanna and 71.41 ± 26.65 g m^{-2} year^{-1} in the seasonal forest. Root:shoot ratio in the savanna was 1.51 and 0.30 in the seasonal forest.

In the savanna, aboveground tree biomass was positively related to the Shannon index (R^2 = 0.25, $P < 0.001$, Fig. 1a) and to functional divergence (R^2 = 0.13, $P < 0.001$, Fig. 1b), but there was no relationship between aboveground biomass and functional richness or functional evenness. In the seasonal forest, aboveground tree biomass was also related to functional divergence (R^2 = 0.24, P = 0.03, Fig. 1c), but not to species diversity, functional richness, or functional evenness. Root biomass and root productivity were not related to species diversity, nor to any of the three components of functional diversity, neither in the savanna nor in the seasonal forest (all $P > 0.05$, graphs not shown).

Discussion

Aboveground standing biomass in the savanna and the seasonal forest could be partially predicted by both species diversity and functional divergence, but not by functional richness and functional evenness. Results were stronger than expected by the literature to controlled experiments and to tropical forests in which species richness and species diversity indices were used as predictors (Balvanera et al. 2006; Ruiz-Jaen and Potvin 2010). Some mechanisms may underlie this trend, such as facilitation between co-occurring species (Brooker et al. 2008), sampling effect, when diverse communities are dominated by highly productive species (Cardinale et al. 2006), and negative soil feedbacks that reduce the biomass in low diversity mixtures (Santiago et al. 2005; Scharfy et al. 2010). However, high values of functional divergence suggest mechanisms of limiting similarity among co-occurring species (Grime 2006; Ricotta and Moretti 2011). More divergent communities might have higher complementarity among species and better use of limiting resources, leading to high biomass production (Tilman et al. 1997; Cardinale et al. 2006). In the savanna and in the seasonal forest, more divergent communities were the most productive, suggesting a high degree of resource differentiation caused by shifts in biotic interactions (Mouchet et al. 2010). We postulate that more efficient use of resources due to niche complementarity may be a mechanism affecting aboveground plant biomass production in these vegetation types.

Functional richness and functional evenness, however, were not related to aboveground plant biomass. Both larger and more evenly distributed functional volumes did not result in better use of resources and higher plant biomass production, contrary to our expectation (Mason et al. 2005; Petchey and Gaston 2006). Functional richness and functional evenness may not be related to plant biomass due to the sensitivity of those indices to the species richness of the plots sampled (Mouchet et al. 2010). In communities with less than 30 species, as in all our sampling plots, functional richness and evenness have a low performance in detecting assembly rules, and might be less effective in detecting changes in community functioning (Mouchet et al. 2010). Thus, functional divergence seems to be a more robust measure and more able to detect community functioning patterns (Mouchet et al. 2010; Pakeman 2013).

The savanna and the seasonal forest had different results relating diversity indices and aboveground biomass. Aboveground biomass was more strongly related to species diversity in the savanna, whilst functional divergence was more important in the seasonal forest. Both indices suggest a better use of limiting resources in communities, but functional divergence assumes causation by shifts in biotic interactions (Mason et al. 2005, 2007). In the savanna, environmental filtering for species composition of the plots – as poor soils, water stress, and fire (Gottsberger and Silberbauer-Gottsberger 2006) – is stronger than in the seasonal forest. In tropical forests, biotic interactions, such as competition among species, is expected to be the main ecological force determining community processes (Gottsberger and Silberbauer-Gottsberger 2006). Our results indicate that biotic interactions played a major role in the seasonal forest, determining aboveground biomass of trees, even though better use of resources also increased tree biomass production in the savanna.

There are few studies testing the effect of diversity on biomass production in natural tropical communities, especially considering belowground biomass and productivity (Balvanera et al. 2006; Cavanaugh et al. 2014). A considerable amount of the biomass in the savanna and in the seasonal forest is allocated belowground and should not be neglected when assessing the carbon pool and productivity of these communities. However, our results suggest that differences in aboveground diversity indices did not affect belowground carbon pool or root productivity. Belowground communities might have up to twice the aboveground plant species richness and different functional diversity indices than aboveground (Hiiesalu et al. 2012), which we did not consider in our analyses. Because sampling belowground diversity and functional traits of plant species is expensive and time-consuming (Milchunas 2009), they might not be widely applied to estimate vegetation biomass and carbon stocks of tropical communities (Mokany et al. 2006). Belowground, plant communities are expected to be driven mainly by abiotic processes (Price et al. 2012), even though root competition and facilitation between species play an important role (Ludwig et al. 2004). Abiotic variables, as soil nutrient availability and fire frequency, might be related to root biomass production and are easier to sample than belowground diversity indices (Milchunas 2009; Price et al. 2012).

In conclusion, diversity was positively related to aboveground plant biomass in the savanna and in the seasonal forest, and testing for multiple diversity indices revealed stronger effect than expected by the literature (Balvanera et al. 2006). Species diversity and functional divergence explained a large amount of the variance of aboveground plant biomass (Balvanera et al. 2006). Increasing complementarity among species and the use of limiting resources might be the underlying mechanism affecting increased aboveground biomass production with increasing plant diversity (Tilman et al. 1997; Loreau and Hector 2001). Belowground biomass was an important share of the total carbon pool and should not be neglected when estimating the impacts caused by climate and land-use changes. Nonetheless, aboveground species or functional diversity indices showed to be inappropriate for estimating the belowground carbon pool, as they were not related to root biomass. Environmental variables might be strongly related to belowground biomass allocation, and their association with diversity indices might be the best tool to estimate the above- and belowground carbon pool in tropical communities.

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References

Balvanera P, Pfisterer AB, Buchmann N, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156. doi: 10.1111/j.1461-0248.2006.00963.x

Brooker RW, Maestre FT, Callaway RM, et al. (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34. doi: 10.1111/j.1365-2745.2007.01295.x

Cardinale BJ, Matulich KL, Hooper DU, et al. (2011) The functional role of producer diversity in ecosystems. Am J Bot 98:572–592. doi: 10.3732/ajb.1000364

Cardinale BJ, Srivastava DS, Emmett Duffy J, et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992. doi: 10.1038/nature05202

Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. J Trop Ecol 14:263–283. doi: 10.1017/S0266467498000212

Cavanaugh KC, Gosnell JS, Davis SL, et al. (2014) Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. Global Ecol Biogeogr 25:563-573. doi: 10.1111/geb.12143

Chave J, Andalo C, Brown S, et al. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99. doi: 10.1007/s00442-005-0100-x

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471. doi: 10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Dantas V de L, Batalha MA, Pausas JG (2013) Fire drives functional thresholds on the savanna-forest transition. Ecology 1–17. doi: 10.1890/12-1629.1.

de Bello F, Leps J, Sebastià M-T (2006) Variations in species and functional plant diversity along climatic and grazing gradients. Ecography 29:801–810. doi: 10.1111/j.2006.0906-7590.04683.x

Delitti WBC, Meguro M, Pausas JG (2006) Biomass and mineralmass estimates in a “cerrado” ecosystem. Braz J Bot 29:531–540. doi: 10.1590/S0100-84042006000400003

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655. doi: 10.1016/S0169-5347(01)02283-2

França H, Ramos-Neto MB, Setzer A (2007) O fogo no Parque Nacional das Emas. Ministério do Meio Ambiente, Brasília

Gottsberger G, Silberbauer-Gottsberger I (2006) Life in the cerrado: a South American tropical seasonal vegetation. Reta, Ulm

Grime PJ (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. J Veg Sci 17:255–260. doi: 10.1111/j.1654-1103.2006.tb02444.x

Higgins SI, Bond WJ, February EC, et al. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology 88:1119–1125. doi: 10.1890/06-1664

Hiiesalu I, Öpik M, Metsis M, et al. (2012) Plant species richness belowground: higher richness and new patterns revealed by next-generation sequencing. Mol Ecol 21:2004–2016. doi: 10.1111/j.1365-294X.2011.05390.x

Hoffmann WA, Adasme R, Haridasan M, et al. (2009) Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. Ecology 90:1326–1337. doi: 10.1890/08-0741.1

Hooper DU, Chapin FS III, Ewel JJ, et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35. doi: 10.1890/04-0922

Jackson RB, Canadell J, Ehleringer JR, et al. (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411. doi: 10.1007/BF00333714

Klumpp K, Soussana JF (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. Glob Change Biol 15:2921–2934. doi: 10.1111/j.1365-2486.2009.01905.x

Köppen W (1931) Grundriss der Klimakunde. Gruyter, Berlin

Krebs CJ (1998) Ecological methodology. Harper Collins, New York

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76. doi: 10.1038/35083573

Ludwig F, Dawson TE, Prins HHT, et al. (2004) Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. Ecol Lett 7:623–631. doi: 10.1111/j.1461-0248.2004.00615.x

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford

Marris E (2005) Conservation in Brazil: the forgotten ecosystem. Nature 437:944–945. doi: 10.1038/437944a

Mason NWH, Irz P, Lanoiselée C, et al. (2008) Evidence that niche specialization explains species–energy relationships in lake fish communities. J Anim Ecol 77:285–296. doi: 10.1111/j.1365-2656.2007.01350.x

Mason NWH, Lanoiselée C, Mouillot D, et al. (2007) Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. Oecologia 153:441–452. doi: 10.1007/s00442-007-0727-x

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118. doi: 10.1111/j.0030-1299.2005

Milchunas DG (2009) Estimating root production: comparison of 11 methods in shortgrass steppe and review of biases. Ecosystems 12:1381–1402. doi: 10.1007/s10021-009-9295-8

Milchunas DG, Mosier AR, Morgan JA, et al. (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: using a new ingrowth method. Plant Soil 268:111–122. doi: 10.1007/s11104-004-0230-7

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root : shoot ratios in terrestrial biomes. Glob Change Biol 12:84–96. doi: 10.1111/j.1365-2486.2005.001043.x

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876. doi: 10.1111/j.1365-2435.2010.01695.x

Myers N, Mittermeier RA, Mittermeier CG, et al. (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi: 10.1038/35002501

Pakeman RJ (2013) Functional trait metrics are sensitive to the completeness of the species' trait data? Method Ecol Evol 5:9–15. doi: 10.1111/2041-210X.12136

Paula S, Pausas JG (2011) Root traits explain different foraging strategies between resprouting life histories. Oecologia 165:321–331. doi: 10.1007/s00442-010-1806-y

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758. doi: 10.1111/j.1461-0248.2006.00924.x

Petchey OL, Hector A, Gaston KJ (2004) How do different measures of functional diversity perform? Ecology 85:847–857. doi: 10.1890/03-0226

Pérez-Harguindeguy N, Díaz S, Garnier E, et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167. doi: 10.1071/BT12225

Potvin C, Mancilla L, Buchmann N, et al. (2011) An ecosystem approach to biodiversity effects: carbon pools in a tropical tree plantation. Forest Ecol Manag 261:1614–1624. doi: 10.1016/j.foreco.2010.11.015

Price JN, Hiiesalu I, Gerhold P, Pärtel M (2012) Small-scale grassland assembly patterns differ above and below the soil surface. Ecology 93:1290–1296. doi: 10.1890/11-1942.1

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43. doi: 10.1016/0040-5809(82)90004-1

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Ann Bot 80:223–230. doi: 10.1006/anbo.1997.0469

Ricotta C, Moretti M (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167:181–188. doi: 10.1007/s00442-011-1965-5

Ruiz-Jaen MC, Potvin C (2010) Tree diversity explains variation in ecosystem function in a Neotropical forest in Panama. Biotropica 42:638–646. doi: 10.1111/j.1744-7429.2010.00631.x

Sala OE, Chapin FS III, Armesto JJ, et al. (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. doi: 10.1126/science.287.5459.1770

Santiago LS, Schuur EAG, Silvera K (2005) Nutrient cycling and plant–soil feedbacks along a precipitation gradient in lowland Panama. J Trop Ecol 21:461–470. doi: 10.1017/S0266467405002464

Scharfy D, Güsewell S, Gessner MO, Venterink HO (2010) Invasion of *Solidago gigantea* in contrasting experimental plant communities: effects on soil microbes, nutrients and plant-soil feedbacks. J Ecol 98:1379–1388. doi: 10.1111/j.1365-2745.2010.01722.x

Scherer-Lorenzen M (2013) The functional role of biodiversity in the context of global change. In: Coomes DA, Burslem DFRP, Simonson WD (eds) Forests and Global Change. Cambridge

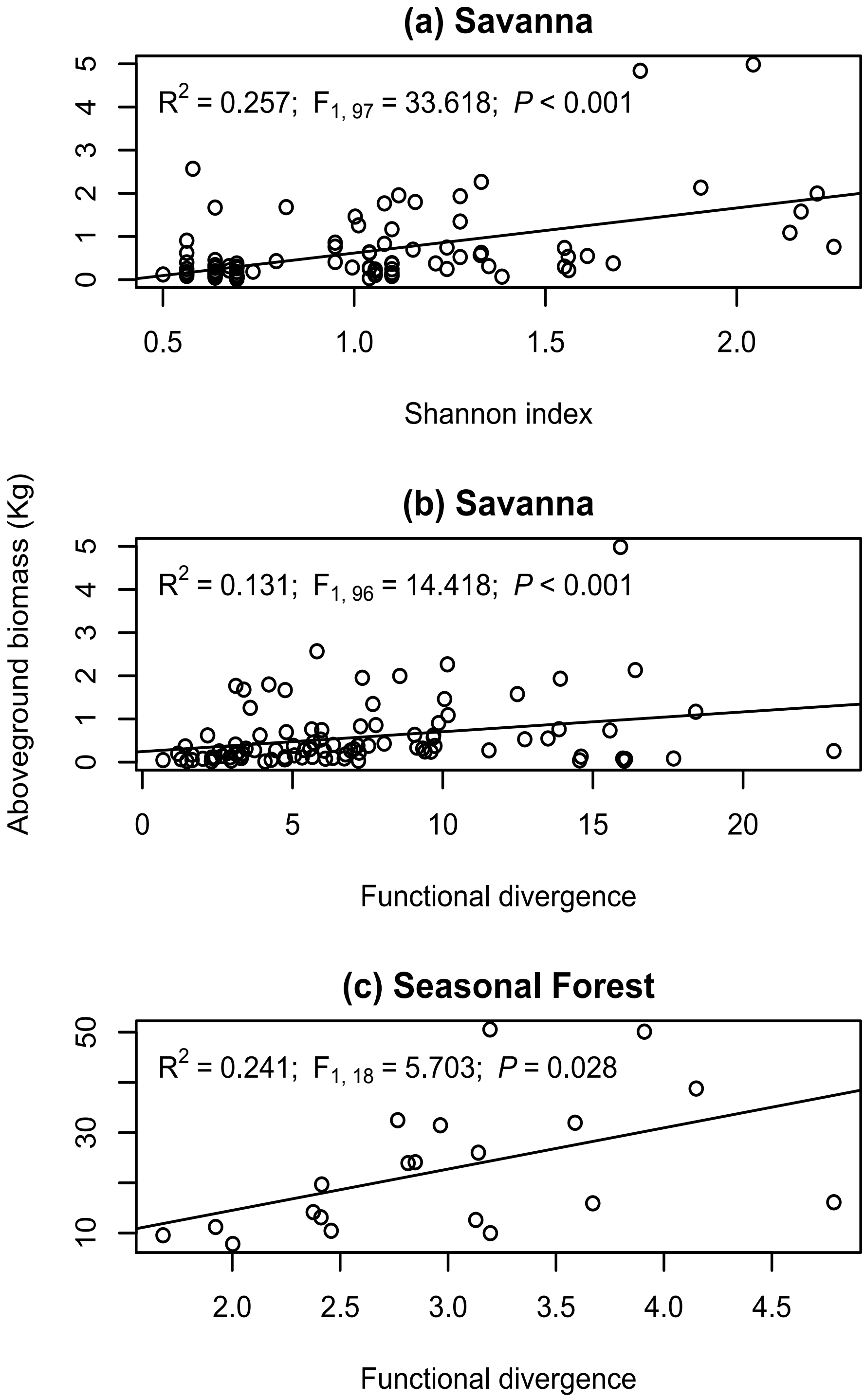
University Press, pp 195–238

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecol Monogr 80:469–484. doi: 10.1890/08-2225.1

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: Theoretical considerations. P Natl Acad Sci 94:1857–1861. doi: 10.1073/pnas.94.5.1857

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. doi: 10.1890/07-1206.

Fig. 1 (a) General linear regression of species diversity (Shannon index) and aboveground biomass in the savanna; (b) General linear regression of functional divergence (FD_Q, Rao 1982) and aboveground biomass in the savanna; and (c) General linear regression of functional divergence and aboveground biomass in the seasonal forest. Graphs show data before log transformation and outliers removal. Aboveground tree biomass was estimated using allometric equations developed for cerrado and dry tropical forests (Delitti et al. 2006; Chave et al. 2005).



(a) Savanna
R2 = 0.257; F1, 97 = 33.618; P < 0.001
Shannon index
(b) Savanna
R2 = 0.131; F1, 96 = 14.418; P < 0.001
Functional divergence
(c) Seasonal Forest
R2 = 0.241; F1, 18 = 5.703; P = 0.028
Functional divergence
Aboveground biomass (Kg)

III - CAPÍTULO 2

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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 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 root productivity in the top 40 cm of soil with an ingrowth core, 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 affecting the root system 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.

Keywords: carbon, cerrado, drought, fire, soil, root

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 considerable part of the plant biomass, and consequently a large amount of the carbon pool, is allocated to the root system (Jackson et al. 1996, 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 in vegetation studies due to the difficulty in obtaining belowground data (Johnson and Matchett 2001; 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; Finér et al. 2011). 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 (Casper and Jackson 1997).

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). 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; Batalha 2011). 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 savannas and tropical forests, 80% of the root biomass is concentrated in the top 100 cm of the soil (Jackson et al. 1996; Castro and Kauffman 1998). According to the few data available, savannas have root biomass of about 15 Mg ha^{-1} and root:shoot ratio of 0.7 (Jackson et al. 1996). In the cerrado, the savanna physiognomies 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 about 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; Girardin et al. 2013).

The lack of information on the root system is partly caused by the difficulty in obtaining data (Gill et al. 2002; Milchunas 2009). In savannas, the difficulty to estimate root biomass is higher than in other biomes, because plant species invest more in deep root allocation (Canadell et al. 1996). 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). Even though all approaches have their limitations, the accuracy and precision of carbon pool estimates of the different vegetation communities have been increasing (Robinson 2007). 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 (Gill et al. 2002; Díaz et al. 2007).

In the cerrado, environmental filters, such as nutrient-poor soils, high fire frequencies, and low water availability, 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; Brauer et al. 2012). Less fertile soils, with less organic matter and nutrient content, should be related to higher root biomass, increasing the nutrient uptake and lowering the effect of the environmental filters (Tateno et al. 2004). Also, fire is a recurrent event impacting the species composition, distribution, and biomass production (Bond and Keeley 2005; Pausas and Keeley 2009). Most cerrado species have subterranean organs that allow them to resist and survive fires (Coutinho 1990). Hence, frequently burned sites might host greater belowground biomass, due to the coarse root organs used to resprout. Topography affects water availability, changing the depth of the ground water level (Oliveira-Filho and Ratter 2002; 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 are expected to be related to higher root biomass and productivity.

Besides the environmental filters, biotic features may also be related to the biomass produced by plant communities (Díaz et al. 2007). For instance, species functional traits may change plant fitness and survival, affecting biomass productivity (Tilman et al. 1997). In the cerrado, plant functional traits that allow better use of limiting soil resources, higher degree of fire resistance, and higher water uptake from the water table during the dry season should allow higher biomass production (Tilman et al. 1997; Cardinale et al. 2006). Moreover, higher functional diversity may be related to different strategies of resource use, leading to higher productivity (Tilman et al. 1997; Ricotta and Moretti 2011). 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 record 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 a total area of 132,941 ha (França et al. 2007) and its climate can be classified as Aw according to Köppen's system (1931), with dry winters and rainy summers. Average rainfall ranges from 1,200 to 2,000 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 physiognomies, 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 x 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, capturing the variation in fire frequency within the park, 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 did not use a stratified random sampling, but placed 20 5 m x 5 m plots, 50 m apart one from the other, in a regular grid.

We sampled 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 x 40 cm. From 40 to 100 cm deep, we extracted a core using an auger of 30 cm diameter (Castro and Kauffman 1998). We sieved the soil with a mesh size of 2 mm and washed the roots to eliminate soil particles. We dried the root samples in the oven at 70°C for 48 hours 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 core 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. The cores had 20 cm diameter, 40 cm deep, and the area inside the cores where root ingrowth occurred were 2.5 cm wide (Milchunas et al. 2005). The soil samples used to fill the cores were taken from the same plot, and the original horizons were kept intact. The mesh limiting the outside part of the cores was made of rigid plastic with holes of 2 mm x 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 and physiognomic variation in the Cerrado domain (Ruggiero et al. 2002; Amorim and Batalha 2006). For each soil 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). We included two variables to assess fire history, 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 two topographic variables, altitude with an altimeter and slope with an inclinometer. In Emas National Park, the higher and the flatter the area, more distant is 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. At the individual level, we sampled performance and functional traits, hereafter called 'functional traits' (Cornelissen et al. 2003). The functional traits, related to plant nutrition and growth and indicative of disturbance levels (Pérez-Harguindeguy et al. 2013), 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 (Cornelissen et al. 2003). Leaf toughness is related to nutritional quality and acts as defence against herbivores (Agrawal et al. 2006). Leaf nutrients are also related to disturbance and assess nutrient limitation to plant growth (Cornelissen et al. 2003). Additionally, 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 with fire 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 plant response to high disturbance level, as fire and drought (Eiten 1972). For each of the 12 functional traits 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 single 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 abundance and discontinuous effects of abiotic and biotic variables, 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 analysed 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 functional trait (Rao 1982). In each step, significant factors were identified for the next stage of the analysis. In the second stage, we combined significant variables, adding and keeping them when they improved model fitness. We selected the best models by parsimony (Garnier et al. 2001; 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 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 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. Functional traits were not highly correlated among them or to soil variables ($R < |0.7|$ in all cases), so all were kept in the analysis. 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 amount of root biomass that were 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 what was reported to other savannas (Jackson et al. 1996). Root biomass and productivity in the cerrado represents a large share of the total carbon pool and total productivity, larger than expected by general extrapolation of other savannas in the world (Jackson et al. 1996; Grace et al. 2006). Hence, the high rates of deforestation, as well as changes in climate and in land-use in the cerrado, will have greater impact on the global carbon balance than expected by extrapolation of data from savannas elsewhere (Jackson et al. 1996; Grace et al. 2006). In the seasonal forest, root biomass and productivity were similar to those found in other tropical forests (Jackson et al. 1996; Aragão et al. 2009). 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 savanna and the seasonal forest in the Cerrado domain will increase the accuracy of estimates of the impacts caused by changes in climate and land-use (Fearnside 2000). Due to the large amount of biomass stocked underground, the loss of vegetation in the Cerrado domain will have a great impact on the carbon pool and should not be neglected (Fearnside 2000; Bustamante et al. 2012).

Root biomass and productivity in the savanna and the seasonal forest could be predicted to variable extent using abiotic and biotic variables. So, the use of models should be considered if one wants to predict the belowground system, because it is cheaper and faster than direct excavation (Milchunas 2009). 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 the main factor responsible for the reduced power. Savannas have an almost continuous herbaceous layer, which shares soil occupation with trees and represents more than half of the plant species (Scholes and Archer 1997; February and Higgins 2010). If we had sampled functional traits of the herbaceous layer as well, explanatory power of the models could have been increased. 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 these variables might be less used to predict the belowground carbon pool in these areas (Gottsberger & Silberbauer-Gottsberger 2006). In some cases, even the identity of the herbaceous layer to species level is not possible (Loiola et al. 2010). 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 with 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, high organic matter content, and low altitude were related to high root biomass and productivity. Extremely clayey soils 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 are the main responsible for cation uptake (Gottsberger and Silberbauer-Gottsberger 2006; Price et al. 2012). The higher availability of cations in the soil leads to a larger fine root productivity in the savanna, maximising cation uptake (Forde and Lorenzo 2001). Soils in the seasonal forest are not expected to be as limited by nutrient content as in the savanna (Ratter et al. 1997), and organic matter did not limit root growth in this case. 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 soil and drought were the main abiotic filter limiting root growth in the savanna, whereas poor soil was the only abiotic filter in the seasonal forest.

Contrary to our expectation, fire frequency did neither affect 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 (Bustamante et al. 2012). Frequent fires have been occurring in the cerrado vegetation for at least 20 million years (Bond and Keeley 2005), and most species are able to store carbohydrates in the root system and resprout after fire. There is a functional stability in the root system under different fire frequencies, possibly due to the same root-growth strategy occurring among most plant species. Functional stability of traits related to fire resistance was also observed along cerrado herbaceous communities submitted to different fire frequencies (Loiola et al. 2010). Alternatively, fine and coarse roots might have different responses to changes in fire frequency. Successive burning promotes tree mortality, decreasing coarse root biomass, and favours grass cover, increasing fine root biomass (Bustamante et al. 2012). If so, a different pattern may be found if different root thicknesses are analysed separately.

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

Biomass production is affected by leaf element concentrations (Zhang et al. 2012). Indeed, leaf potassium and leaf nitrogen affected root biomass and productivity in the savanna and in the seasonal forest, respectively. Even though cerrado species do not have high variability in nutrient concentration due to strong nutrient limitation in the soil (Cianciaruso et al. 2013), the variability in leaf potassium and in leaf nitrogen concentrations affected root biomass production. 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, nutritional quality of the leaves, and to the nitrogen availability in the environment (Westoby et al. 2002) (Cornelissen et al. 2003). In the seasonal forest, low leaf nitrogen content resulted in low root biomass, but high root productivity. Nitrogen limited the total root biomass, as expected (Ladwig et al. 2011), but increased fine root productivity, the main responsible for foraging and nutrient uptake (Price et al. 2012). Nitrogen variability affected the belowground biomass investment in the seasonal forest, with different effects on the carbon pool and on the carbon uptake. Hence, potassium and nitrogen affected the root production to maximise the uptake of limiting resources

(Price et al. 2012), and they might be used to estimate root biomass and productivity in the Cerrado domain.

Additionally, high divergence of two functional traits, leaf toughness and bark thickness, were positively correlated to root biomass and productivity in the savanna, but not to the root system in the seasonal forest. High functional 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 also greater complementarity among species led to higher root biomass and productivity in our study.

Our models are applicable to other cerrado areas, because 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, consequently, high species turnover (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 did not include species abundances, since they vary sharply from site to site (Gottsberger and Silberbauer-Gottsberger 2006). Moreover, we excluded from our analysis the last step, which search for discontinuous effects of abiotic or biotic effects on the ecological properties studied, because all our models had been significant (Díaz et al. 2007).

In conclusion, the root system comprises an important share of the carbon pool of the savanna and the semidecidous seasonal forest in the Cerrado domain. Its carbon stock is large and should not be neglected when estimating the impacts caused by climate and land-use changes (Fearnside 2000). Deforestation of tropical vegetation is a major source of greenhouse gases, and the Cerrado is one of the hotspots of biodiversity conservation in the world (Myers et al. 2000). In this sense, predicting the belowground stock of carbon in this area is of great importance to estimate and minimise the impacts caused by deforestation (Bustamante et al. 2012). 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). We found significant models based on field measurements that are simpler than direct excavation methods. The variance explained by these models might be improved by including traits of non-woody vegetation, especially in the savannas. Nevertheless, the approach suggested here is valuable to estimate the root system in savannas and tropical forests within the Cerrado domain.

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References

Agrawal AA, Lau JA, Hambäck PA (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. Q Rev Biol 81:349–376. doi: 10.1086/511529?uid=2&uid=4&sid=21103104553453

Amorim PK, Batalha MA (2006) Soil characteristics of a hyperseasonal cerrado compared to a seasonal cerrado and a floodplain grassland: implications for plant community structure. Braz J Biol 66:661–670. doi: 10.1590/S1519-69842006000400010

Aragão LEOC, Malhi Y, Metcalfe DB, et al. (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences 6:2759–2778. doi: 10.5194/bg-6-2759-2009

Balvanera P, Pfisterer AB, Buchmann N, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156. doi: 10.1111/j.1461-0248.2006.00963.x

Batalha MA (2011) O cerrado não é um bioma. Biota Neotrop 11:1–4. doi: 10.1590/S1676-06032011000100001

Bond WJ, Keeley JE (2005) Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394. doi: 10.1016/j.tree.2005.04.025

Brauer VS, Stomp M, Huisman J (2012) The nutrient-load hypothesis: patterns of resource limitation and community structure driven by competition for nutrients and light. Am Nat 179:721–740. doi: 10.1086/665650

Bustamante MMC, Brito DQ, Kozovits AR, et al. (2012) Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). Plant Ecol 213:795–808. doi: 10.1007/s11258-012-0042-4

Canadell J, Jackson RB, Ehleringer JR, et al. (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595. doi: 10.1111/j.1744-7909.2007.00633.x

Cardinale BJ, Srivastava DS, Emmett Duffy J, et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992. doi: 10.1038/nature05202

Casper BB, Jackson RB (1997) Plant competition underground. Annu Rev Ecol Syst 28:545–570. doi: 10.1146/annurev.ecolsys.28.1.545

Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. J Trop Ecol 14:263–283. doi: 10.1017/S0266467498000212

Cianciaruso MV, Silva IA, Manica LT, Souza JP (2013) Leaf habit does not predict leaf functional traits in cerrado woody species. Basic Appl Ecol 14:404–412. doi: 10.1016/j.baae.2013.05.002

Cornelissen JHC, Lavorel S, Garnier E, et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335. doi: 10.1071/BT02124

Coutinho LM (1990) Fire in the ecology of the Brazilian cerrado. In: Goldammer JC (ed) Fire in the tropical biota. Springer, Berlin, pp 81–103

Dantas VL, Pausas JG, Batalha MA, et al. (2013) The role of fire in structuring trait variability in Neotropical savannas. Oecologia 171:487–494. doi: 10.1007/s00442-012-2431-8

Di Iorio A, Montagnoli A, Scippa GS, Chiatante D (2011) Fine root growth of *Quercus pubescens* seedlings after drought stress and fire disturbance. Environ Exp Bot 74:272–279. doi: 10.1016/j.envexpbot.2011.06.009

Díaz S, Lavorel S, de Bello F, et al. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. P Natl Acad Sci 104:20684–20689. doi: 10.1073/pnas.0704716104

Eiten G (1972) The Cerrado vegetation of Brazil. Bot Rev 38:201–341. doi: 10.1007/BF02859158

Fearnside PM (2000) Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. Climatic Change 46:115–158. doi: 10.1023/A:1005569915357

Fearnside PM, Laurance WF (2004) Tropical deforestation and greenhouse-gas emissions. Ecol Appl 14:982–986. doi: 10.1890/03-5225

February EC, Higgins SI (2010) The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. S Afr J Bot 76:517–523. doi: 10.1016/j.sajb.2010.04.001

Finér L, Ohashi M, Noguchi K, Hirano Y (2011) Factors causing variation in fine root biomass in forest ecosystems. Forest Ecol Manage 261:265–277. doi: 10.1016/j.foreco.2010.10.016

Forde B, Lorenzo H (2001) The nutritional control of root development. Plant Soil 232:51–68. doi: 10.1023/A:1010329902165

França H, Ramos-Neto MB, Setzer A (2007) O fogo no Parque Nacional das Emas. Ministério do Meio Ambiente, Brasília

Garnier E, Cortez J, Billès G, et al. (2004) Plant functional markers capture ecosystem properties during secondary sucession. Ecology 85:2630–2637. doi: 10.1890/03-0799

Garnier E, Laurent G, Bellmann A, et al. (2001) Consistency of species ranking based on functional leaf traits. New Phytol 152:69–83. doi: 10.1046/j.0028-646x.2001.00239.x

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13–31. doi: 10.1046/j.1469-8137.2000.00681.x

Gill RA, Polley HW, Johnson HB, et al. (2002) Nonlinear grassland responses to past and future atmospheric CO_2. Nature 417:279–282. doi: 10.1038/417279a

Girardin CAJ, Aragão LEOC, Malhi Y, et al. (2013) Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. Global Biogeochem Cy 27:252–264. doi: 10.1029/2011GB004082

Gottsberger G, Silberbauer-Gottsberger I (2006) Life in the cerrado: a South American tropical seasonal vegetation. Reta, Ulm

Grace J, Jose JS, Meir P, et al. (2006) Productivity and carbon fluxes of tropical savannas. J Biogeorgr 33:387–400. doi: 10.1111/j.1365-2699.2005.01448.x

Higgins SI, Bond WJ, February EC, et al. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology 88:1119–1125. doi: 10.1890/06-1664

Hoffmann WA, Adasme R, Haridasan M, et al. (2009) Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. Ecology 90:1326–1337. doi: 10.1890/08-0741.1

Jackson RB, Canadell J, Ehleringer JR, et al. (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411. doi: 10.1007/BF00333714

Johnson LC, Matchett JR (2001) Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389. doi: 10.1890/00129658(2001)082[3377:FAGRBP]2.0.CO;2

Klumpp K, Soussana JF (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. Glob Change Biol 15:2921–2934. doi: 10.1111/j.1365-2486.2009.01905.x

Köppen W (1931) Grundriss der Klimakunde. Gruyter, Berlin

Körner C (2003) Slow in, rapid out - Carbon flux studies and Kyoto targets. Science 300:1242–1243. doi: 10.1126/science.1084460

Krebs CJ (1998) Ecological methodology. Harper Collins, New York

Ladwig LM, Collins SL, Swann AL, et al. (2011) Above- and belowground responses to nitrogen addition in a Chihuahuan desert grassland. Oecologia 169:177–185. doi: 10.1007/s00442-011-2173-z

Lilienfein J, Wilcke W, Zimmermann R, et al. (2001) Nutrient storage in soil and biomass of native Brazilian Cerrado. J Plant Nutr Soil Sc 164:487–495. doi: 10.1002/1522-2624(200110)164:5<487::AID-JPLN487>3.0.CO;2-I

Loiola P de P, Cianciaruso MV, Silva IA, Batalha MA (2010) Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. Flora 205:674–681. doi: 10.1016/j.flora.2010.04.006

Mason NWH, Lanoiselée C, Mouillot D, et al. (2007) Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. Oecologia 153:441–452. doi: 10.1007/s00442-007-0727-x

Milchunas DG (2009) Estimating Root Production: Comparison of 11 methods in shortgrass steppe and review of biases. Ecosystems 12:1381–1402. doi: 10.1007/s10021-009-9295-8

Milchunas DG, Mosier AR, Morgan JA, et al. (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: using a new ingrowth method. Plant Soil 268:111–122. doi: 10.1007/s11104-004-0230-7

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. Glob Change Biol 12:84–96. doi: 10.1111/j.1365-2486.2005.001043.x

Myers N, Mittermeier RA, Mittermeier CG, et al. (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi: 10.1038/35002501

Myneni RB, Dong J, Tucker CJ, et al. (2001) A large carbon sink in the woody biomass of Northern forests. P Natl Acad Sci 98:14784–14789. doi: 10.1073/pnas.261555198

Oliveira RS, Bezerra L, Davidson EA, et al. (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. Funct Ecol 19:574–581. doi: 10.1111/j.1365-2435.2005.01003.x

Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the Cerrado Biome. In: Oliveira PS, Marquis RJ (eds) The Cerrados of Brazil: ecology and natural history of a Neotropical savanna. Columbia University Press, New York, pp 91–120

Pandey CB, Singh JS (1992) Rainfall and grazing effects on net primary productivity in a tropical savanna, India. Ecology 73:2007–2021. doi: 10.2307/1941451

Pausas JG, Keeley JE (2009) A burning story: the role of fire in the history of life. BioScience 59:593–601. doi: 10.1525/bio.2009.59.7.10

Pärtel M, Hiiesalu I, Öpik M, Wilson SD (2012) Below-ground plant species richness: new insights from DNA-based methods. Funct Ecol 26:775–782. doi: 10.1111/j.1365-2435.2012.02004.x

Pérez-Harguindeguy N, Díaz S, Garnier E, et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167. doi: 10.1071/BT12225

Prado C (2013) Aquisição de nutrientes minerais na solução do solo. Tipografia Editora Expressa, São Carlos

Price JN, Hiiesalu I, Gerhold P, Pärtel M (2012) Small-scale grassland assembly patterns differ above and below the soil surface. Ecology 93:1290–1296. doi: 10.1890/11-1942.1

Raij B, Quaggio JA, Cantarella H, Ferreira ME, Lopes AS, Bataglia OC (1987) Análise química de solos para fins de fertilidade. Fundação Cargill, Campinas

Ramos-Neto MB, Pivello VR (2000) Lightning fires in a Brazilian savanna national park: rethinking management strategies. Environ Manage 26:675–684. doi: 10.1007/s002670010124

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43. doi: 10.1016/0040-5809(82)90004-1

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian Cerrado vegetation and threats to its biodiversity. Ann Bot 80:223–230. doi: 10.1006/anbo.1997.0469

Ribeiro SC, Fehrmann L, Soares CPB, et al. (2011) Above- and belowground biomass in a Brazilian Cerrado. Forest Ecol Manage 262:491–499. doi: 10.1016/j.foreco.2011.04.017

Ricotta C, Moretti M (2011) CWM and Rao’s quadratic diversity: a unified framework for functional ecology. Oecologia 167:181–188. doi: 10.1007/s00442-011-1965-5

Robinson D (2007) Implications of a large global root biomass for carbon sink estimates and for soil carbon dynamics. P Roy Soc Lond B Bio 274:2753–2759. doi: 10.1126/science.1130168

Rossatto DR, Silva LCR, Villalobos-Vega R, Sternberg LSL, Franco AC (2012) Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. Environ Exp Bot 77:259–266. doi: 10.1016/j.envexpbot.2011.11.025

Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. Plant Ecol 160:1–16. doi: 10.1023/A:1015819219386

Sankaran M, Hanan NP, Scholes RJ, et al. (2005) Determinants of woody cover in African savannas. Nature 438:846–849. doi: 10.1038/nature04070

Schenk HJ, Jackson RB (2002) The global biogeography of roots. Ecol Monogr 72:311–328. doi: 10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annu Rev Ecol Syst 28:517–544. doi: 10.1146/annurev.ecolsys.28.1.517

Tateno R, Hishi T, Takeda H (2004) Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. Forest Ecol Manage 193:297-306. doi: 10.1016/j.foreco.2003.11.011

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. Proc Natl Acad Sci 94:1857–1861. doi: 10.1073/pnas.94.5.1857

Tilman D, Reich PB, Knops J, et al. (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843–845. doi: 10.1126/science.1060391

Villéger S, Mason NWH, Mouillot D (2008) New Multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. doi: 10.1890/07-1206.1

Westoby M, Falster DS, Moles AT, et al. (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159. doi: 10.1146/annurev.ecolsys.33.010802.150452

Zhang S-B, Zhang J-L, Slik JWF, Cao K-F (2012) Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment. Glob Ecol Bioeogr 21:809–818. doi: 10.1111/j.1466-8238.2011.00729.x

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.

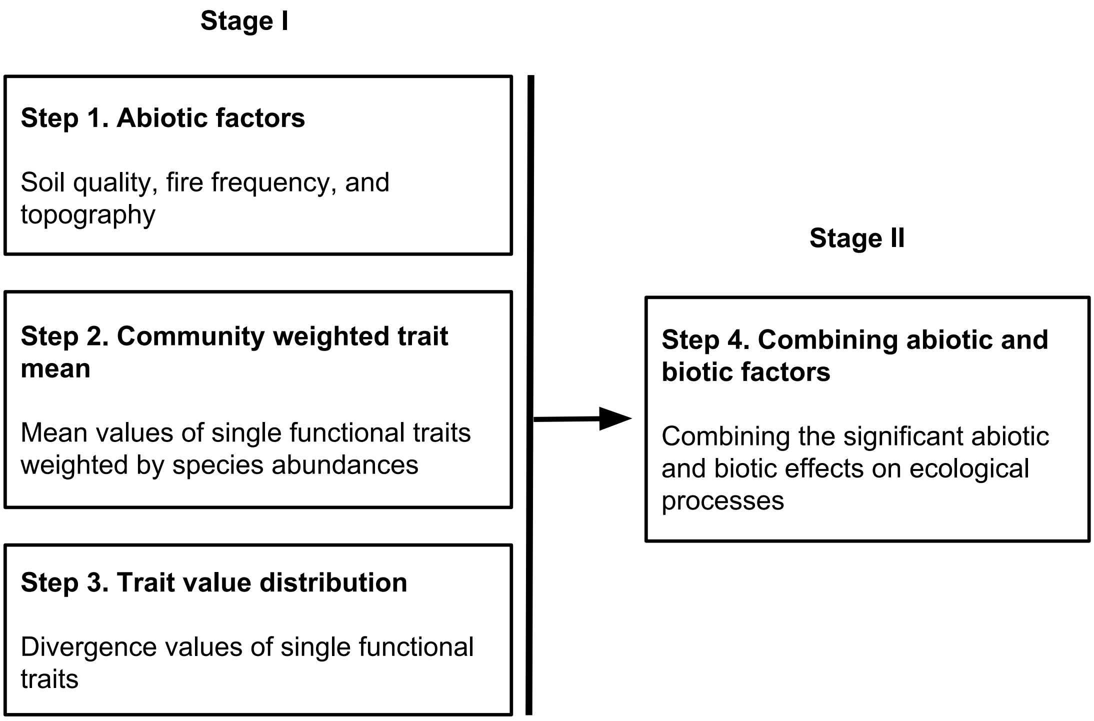
Stage I
Step 1. Abiotic factors
Soil quality, fire frequency, and topography
Step 2. Community weighted trait mean
Mean values of single functional traits weighted by species abundances
Step 3. Trait value distribution
Divergence values of single functional traits
Stage II
Step 4. Combining abiotic and biotic factors
Combining the significant abiotic and biotic effects on ecological processes

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 analysed 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

Electronic Supplementary Material

Table 1. Final models predicting root biomass and productivity in the savanna and in the seasonal forest using standardized variables, 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)	- 0.31 altitude – 0.18 tortuosity - 0.29 leaf potassium + 0.15 leaf toughness divergence	24
ln (root biomass seasonal forest)	- 5.05 clay - 2.20 bark thickness + 3.37 leaf nitrogen	56
ln (root productivity savanna)	- 0.26 clay + 0.26 OM - 0.17 leaf potassium + 0.18 bark thickness divergence	16
ln (root productivity seasonal forest)	- 0.35 leaf nitrogen - 0.63 top kill	55

Table 2. Final models predicting root biomass and productivity in the savanna and in the seasonal forest including the species abundances, 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**	$\mathbf{R^2_{adj}}$
ln (root biomass savanna)	10.65 - 0.05 altitude - 2.95 tortuosity - 0.07 leaf potassium + 0.05 leaf toughness divergence + 0.25 *E. suberosum*	24
ln (root biomass seasonal forest)	5.87 - 0.004 clay - 0.24 bark thickness + 0.10 leaf nitrogen + 3.06 *T. laevigata*	66
ln (root productivity savanna)	1.75 - 0.006 clay + 0.006 OM - 0.02 leaf potassium + 0.11 bark thickness divergence + 0.21 *P. ramiflora*	26
ln (root productivity seasonal forest)	3.62 - 0.08 leaf nitrogen - 4.01 top kill	55

IV - CAPÍTULO 3

Artigo formatado para ser submetido ao periódico Austral Ecology

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

Short title: Roles of resource and disturbance in root

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Abstract

Savannas – along with tropical forests and deserts – are among the most unknown biomes concerning the belowground system. Root biomass might be influenced by the availability of limiting resources and by the type and intensity of disturbances. Fine and coarse roots should be affected differently by nutrient availability and disturbance intensity: 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 poor soils, drought, high fire frequencies, and plant resistance to fire. We sampled the root biomass, environmental variables, and functional traits of resistance to fire in 100 plots in Central Brazil, and used structural equation modeling to test our hypothesis. Shallow root biomass, from 0 to 20 cm deep, was not caused by resource availability or by disturbances, as fire or drought. Biotic interactions were not considered in our study, but they may impact shallow root biomass. In the deep layer, from 20 to 100 cm deep, we identified soil fertility and recent fires as the main environmental factors causing changes in fine and coarse root biomass in the cerrado. Lack of nutrients in the soil caused higher fine root biomass, increasing 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 the plots, with less coarse root biomass. Accordingly to our expectation, fine roots were mostly affected by nutrient availability in the soil, whereas coarse roots were more related disturbance, in our case, recent fires.

Keywords: drought, fire, functional traits, soil fertility, structural equation modeling

Introduction

Savannas have a large belowground system compared to other biomes, accounting for nearly 40% of total plant biomass in these communities (Jackson et al. 1996; Ribeiro et al. 2011). Nevertheless, data on root biomass are scarce as sampling methods are often unverifiable and have low number of replicates (Mokany et al. 2006). For this reason, savannas – along with tropical forests and deserts – are among the most unknown biomes concerning the belowground system (Scholes and Archer 1997; Mokany et al. 2006). Root biomass might be influenced by the availability of limiting resources and by the type and intensity of disturbances (February et al. 2013). Resource availability and disturbance frequency should support different survival strategies among plant species according to root investment and, thus, support changes in the belowground carbon pool and uptake (Paula and Pausas 2011). The impact of limiting resources and disturbances on root biomass is not clear, especially if we take into account their effects on fine and coarse root biomass separately (February et al. 2013).

Fine and coarse root biomass contributes to resource uptake and survival after disturbance, and, therefore, is critical for plant communities (Grime et al. 1986; Malamy 2005). Fine roots, up to 2 mm wide, are the main responsible for water and nutrient uptake, and might respond strongly to their availability in the soil (Jackson et al. 1997; Forde and Lorenzo 2001). They are faster to produce than coarse roots and have high turnover rate in tropical areas, being responsible for most of the carbon uptake in those communities (Gill and Jackson 2000). Coarse roots are more costly to produce, but they have greater transport capacity, are less vulnerable to physical damage, and are longer-lived than fine roots (Fitter 1987). Coarse roots have a structural role and might work as resource storage organs used to resprout after disturbances (Coutinho 1990; Pausas and Keeley 2009). In this sense, fine and coarse root biomass should be affected differently by nutrient availability and disturbance intensity: the former should be more responsive to resource supplies, whilst the latter should be related to changes in disturbance frequency (Lei et al. 2012; Pärtel et al. 2012).

We studied the roles of resource distribution and disturbance intensity in fine and coarse root biomass of savanna physiognomies of the cerrado vegetation, in central Brazil (Gottsberger and Silberbauer-Gottsberger 2006). The most important environmental filters affecting the cerrado are poor soils, drought, and high fire frequencies (Gottsberger and Silberbauer-Gottsberger 2006). These environmental conditions affect plant growth and the carbon pool and uptake of the vegetation, above- and belowground (Bustamante et al. 2012; Price et al. 2012). Fine roots should be mostly affected by nutrient availability in the soil, whereas coarse roots should be more related to drought and fire frequency (Oliveira et al. 2005; Bustamante et al. 2012). Understanding how fine and coarse roots are affected by soil nutritional quality, water availability, and fire frequency may help to explain community functioning, species coexistence, and carbon pool allocation in savannas (Paula and Pausas 2011; February et al. 2013).

Availability of nutrients in soil, such as nitrogen, phosphorus, and cation exchange capacity, is determinant for biomass production, especially in poor soils (February et al. 2013). Soils in cerrado have low cation availability and high aluminum content, affecting competitive interactions and limiting plant biomass and productivity (Tilman et al. 1997; Forde and Lorenzo 2001). Nutrient-rich zones should stimulate the growth of fine roots and increase nutrient uptake, whereas low nutrient content zones should affect negatively fine root growth (Price et al. 2012). Nutrient availability is positively related to root ramification, length, and high fine root biomass of grasses and herbs, but it has no effect on coarse root biomass (Whiting et al. 2000; Lei et al. 2012). Moreover, in acidic soils, aluminum is solubilised and represents an important limitation to plant growth, reducing fine root biomass (Delhaize and Ryan 1995). In this sense, we expected that high nitrogen and phosphorus availability, and high cation exchange capacity, a surrogate for soil fertility, along with low aluminum content, should increase fine root biomass and have no effect on coarse root biomass.

Among the environmental disturbances that might affect biomass production in cerrado communities, the most important are drought and fire (Gottsberger and Silberbauer-Gottsberger 2006). Low water availability might overcome the limitation caused by nutrient deficiency in soil and is related to decrease of plant growth, also belowground (Ladwig et al. 2012). Cerrado tree species can produce deep roots to reach the groundwater, allowing tree growth and survival during the dry season (Oliveira et al. 2005). 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 system at the community level may help plant communities to overcome the strong limitation caused by drought. In the cerrado, topography affects water availability, changing the depth of the groundwater (Oliveira-Filho and Ratter 2002; Rossatto et al. 2012). Deep groundwater represents larger soil volume available for root growth, and they are found in high altitude and flat terrain (Rossatto et al. 2012). So, we expected high altitude and flat terrain to be related with higher deep fine and coarse root biomass at community level, increasing water uptake and diminishing the impact of drought on plant communities (Rossatto et al. 2012).

Fire is a main disturbance in savanna communities around the world in a long history that lasts nearly 20 million years, affecting both above- and belowground plant biomass (Bond et al. 2005). As long as fire frequency is increasing in the last decades due to human activities, it is important to predict how plant communities and the carbon pool will respond in this new scenario of frequent fires (Pausas and Keeley 2009). Fire consumes aboveground biomass and postpones the peak of fine root growth (Grime 1979; Di Iorio et al. 2011). Moreover, a common strategy to survive frequent burning is to resprout after fire, using carbohydrates stored in the root system, usually coarse roots (Pausas and Keeley 2009). Species able to resprout should be common in fire-prone communities, and their belowground system are expected to be deeper and coarser than in communities protected from fire (Verdaguer and Ojeda 2002; Paula and Pausas 2011). Consequently, we expected that high fire frequencies would decrease fine root biomass (Pausas and Keeley 2009; Di Iorio et al. 2011). Fire might also have an indirect effect on root biomass, by increasing soil fertility via nutrients deposited as ashes (Coutinho 1990; Silva and Batalha 2008).

In fire-prone communities, plants have functional traits that promote fire resistance, such as the ability to resprout from the root system and the production of a seed bank that germinates after burning (Pausas et al. 2004). Less resistant plants should be more strongly impacted by fire and delay their biomass reconstruction, above- and belowground (Zwicke et al. 2013). Larger values of height, basal area, and bark thickness represent high fire resistance, as they diminish the damage caused by fire, allowing a fast recovery of the plant (Gignoux et al. 1997). Height and basal area change fire resistance to surface fires, the most common type of fire in the cerrado (Gottsberger and Silberbauer-Gottsberger 2006). Taller and thicker plants preserve their leaves from fire and are better protected from high temperatures (Bond et al. 2012). Bark thickness insulates the inside living tissues against high temperatures and avoids death of aboveground organs (Hoffmann et al. 2009). If so, fire-resistant plants, with higher values of height, basal area, and bark thickness, should be less damaged by fire and have higher biomass, above- and belowground.

Our goal was to test whether soil quality (assessed through cation and aluminum 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 is not uniform. We expected that higher soil quality, 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 in our study site.

Material and 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 x 5 m plots in the savanna, following a stratified random sampling design (Krebs 1998) with ten strata of fire frequency, from the absence of fire to annual fire from 1984 to 2010, when we started sampling the data. In each plot, we sampled the root biomass to the depth of 100 cm. We extracted two soil monoliths of 40 cm x 40 cm x 20 cm, until 40 cm deep. From 40 to 100 cm deep, we extracted a core using a 30 cm diameter auger (Castro and Kauffman 1998). We separated root sample in two layers, shallow and deep, with the shallow layer comprising the first 20 cm of soil and the deep layer lying from 20 to 100 cm deep (Castro and 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 hours and weighted them.

We collected soil samples in each plot and assessed nitrogen, phosphorus, cation exchange capacity, and aluminum 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 measured the altitude and inclination of each plot using an altimeter and an inclinometer. High altitudes and flat terrain are related to deep groundwater and should support larger root biomass (Castro and Kauffman 1998). We considered the years elapsed since the last fire that reached each plot, as a measure of recent fire. Moreover, we identified all woody individuals with stem diameter at soil level equal to or larger than 3 cm and sampled three functional traits as surrogates of fire resistance: basal area (m^2), tree height (m), and bark thickness (mm). Each trait value was the average of that trait for all individuals in a plot. The state of these traits represents the plastic response of plants to fire, and functional traits should differ among fire regimes (Carvalho and 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 structural equation modeling to test a model connecting soil fertility, water availability, fire frequency, and plant resistance to fine and coarse root biomass. We proposed one a priori structural equation model (Fig. 1) and tested it to fine and coarse roots biomass in two different depths: shallow (0 to 20 cm) and deep (20 to 100 cm), using the 'lavaan' package (Rosseel 2012) for R (R Core Team 2013). We did a confirmatory factor analysis with the variables that cause the latent variables (Carvalho and Batalha 2013). To estimate the parameters and assess the fit of the structural equation model, we used maximum likelihood estimation (ML). We used a robust estimator of standard errors to account for deviations from multivariate normality in our data.

Results

The structural equation models to shallow root biomass exhibited a poor fit with the data, both to fine and coarse root biomass ($P < 0.001$, figures not shown). The model to deep fine root biomass was marginally significant ($\chi^2 = 50.58$, df = 35, $P = 0.04$, Fig 2). However, the model to deep coarse root fitted the data well ($\chi^2 = 44.71$, d.f. = 35, $P = 0.12$, Fig. 3). The latent variables exhibited strong fit with the data, and all variables showed significant path coefficients. The paths connecting aluminum content, topographic variables, and fire resistance to root biomass were non-significant in all cases ($P > 0.05$). Aluminum content had a negative effect on soil fertility in both cases, as we expected (Standardised estimator = 0.04, $P < 0.001$ for both deep fine and coarse root models). Also, soil fertility was positively affected by recent fire in both models (Standardised estimator = 0.02, $P < 0.001$ for both deep fine and coarse root models). Soil fertility had a negative effect on fine root biomass (Standardised estimator = 0.43, $P = 0.02$) and no effect on coarse root biomass (Standardised estimator = 0.70, $P = 0.92$). Recent fire had no effect on fine root biomass (Standardised estimator = 0.09, $P = 0.68$), but influenced negatively deep coarse root biomass (Standardised estimator = 0.16, $P = 0.02$). Fire resistance was not related to recent fire in any case (Standardised estimator = 0.10, $P = 0.26$ for the deep fine root model; and Standardised estimator = 0.18, $P = 0.98$ for the deep coarse root model).

Discussion

Among the resources and disturbances we analysed, soil fertility was the only that affected fine root biomass below 20 cm deep. Contrary to our expectation, however, cerrado species increased their fine root biomass in patches with small cation availability, and soil fertility had no influence on coarse root biomass, as we expected (Forde and Lorenzo 2001). Fine roots are the main responsible for cation uptake from the soil and, thus, more fine roots should increase the cation uptake (Forde and Lorenzo 2001). Even though most studies report higher fine root biomass in rich soil patches (Robinson 1994; Price et al. 2012), different responses might be given for the same environmental stimulus (Forde and Lorenzo 2001). Belowground fine root production was reported to increase towards low nitrogen availability (Tateno et al. 2004). In nutrient-limited sites, as the cerrado, abiotic forces might filter species with trait values that allow them to overcome the limitations imposed by the environment (Keddy 1992; Tateno et al. 2004).

Additionally, soil fertility was caused by differences in recent fires and aluminum content. Recent fires caused higher soil fertility, as we expected. The same result was found in studies in cerrado and in African savannas, with recent fires increasing cation availability (Jensen et al. 2001; Carvalho et al. 2014). Even though part of the chemicals and particles are lost in the smoke by volatilisation, part of the nutrients is deposited in the soil as ashes and increases the cation availability (Coutinho 1990). Furthermore, plants lose young leaves after burning and litter with high nutrient content accumulates on the soil, increasing soil fertility (Rodríguez et al. 2009). High aluminum content did not directly affect root biomass but indirectly, as it decreased soil fertility. Aluminum is related to acidic soils, to low concentration of nutrients in the soil, and to low density of woody individuals, and is expected to have a negative impact on root biomass (Goodland and Pollard 1973; Fierer and Jackson 2006). However, many plant species exhibit variability in aluminum sensitivity that may allow them to resist the toxicity affecting root growth (Kochian 1995). This might be the case in cerrado communities, as we did not observe a causal relationship between high aluminum content and low fine or coarse root biomass.

Differences in water availability also did not affect fine or coarse root biomass in the cerrado. We expected that deep groundwater, found in high altitude and flat terrains, would increase the soil volume available to the root system, increasing root growth and water uptake (Rossatto et al. 2012). In Emas, water availability is determinant of the vegetation structure, increasing the functional diversity of the plots (Carvalho et al. 2014). When we considered the entire root system in the analysis, considering both fine and coarse roots, we found that the altitude of the plots was related to total root biomass. 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 belowground carbon pool, it was only revealed when we accounted for the cumulative effect on fine and coarse root biomass.

In contrast to the effect of water availability, the effect of fire on root biomass could only be observed when we separated the fine and the coarse roots. Contrary to what we expected, recent fires decreased coarse root biomass and had no effect on fine root biomass below 20 cm deep. Even though fire is expected to stimulate belowground storage in coarse root organs, it might favour grasses, with less coarse root biomass, instead of trees (Bond and Keeley 2005; February et al. 2013). Additionally, we expected that fire would postpone the peak of fine root growth, leading to less fine root biomass in communities submitted to recent fires (Di Iorio et al. 2011). However, the effect of disturbances on fine root biomass, as drought and fire, may be missed as fine roots have high turnover in tropical sites (Gill and Jackson 2000). The replacement of lost fine roots can happen in the same season that the disturbance occurred, and leave no trace on the fine root biomass after one year (Pärtel et al. 2012).

Plant functional resistance, assessed through functional traits related to fire, 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 traits in cerrado (Carvalho et al. 2014), giving support to the insurance theory, which states that plant species composition might change without promoting loss of functional diversity or community processes (Yachi and Loreau 1999; Loreau and Hector 2001). Other studies in cerrado also show that fire is not related to different functional diversity of the communities, although differences in aboveground biomass and species composition are related to different fire frequencies (Cianciaruso et al. 2010, 2012; Carvalho et al. 2014). In the cerrado, plant species seem to be selected by fire at regional scale, and changes in local fire frequency do not imprint differences in functional strategies, such as plant resistance to fire.

Shallow root biomass, in the top 20 cm of soil, is a large portion of the carbon pool, near 80% of the total root biomass (Jackson et al. 1996). Contrary to our expectation, shallow root biomass in cerrado was not caused by resource availability or by disturbances, as fire or drought. Even though abiotic factors are expected to be the main determinants of belowground biomass production (Price et al. 2012), the main abiotic filters of cerrado did not affect root biomass in the first 20 cm of soil. Biotic interactions, as competition and facilitation, change species similarity and impact community properties, especially under nutritional limited sites (Stubbs and Wilson 2004). Biotic interactions were not considered in our study, but they may impact shallow root biomass. Moreover, the herbaceous layer is important in cerrado sites, since it 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 functional resistance to fire might be determinant to the shallow root biomass investment.

To understand how resource availability and disturbance interact with each other and cause changes in the community functioning might be critical for conservation of diversity, properties and processes of the natural communities (Srivastava and Vellend 2005; Grace et al. 2007). Many aspects of the environment may be interconnected through different paths and affect the carbon pool and cycling (Díaz et al. 2007). Using structural equation modeling, we were able to identify soil fertility and recent fires as the main environmental factors causing changes, respectively, in fine and coarse root biomass in the cerrado. Plant response to the lack of nutrients in the soil increases fine root biomass, increasing 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 the plots. Accordingly to our expectation, fine roots were mostly affected by nutrient availability in the soil, whereas coarse roots were more related disturbance, in our case, recent fires.

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References

Bond W. J., Cook G. D. & Williams R. J. (2012) Which trees dominate in savannas? The escape hypothesis and eucalypts in northern Australia. *Austral Ecol*. **37**, 678–685.

Bond W. J. & Keeley J. E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol Evol*. **20**, 387–394.

Bond W. J., Woodward F. I. & Midgley G. F. (2005) The global distribution of ecosystems in a world without fire. *New Phytol*. **165**, 525–538.

Bustamante M. M. C., Brito D. Q., Kozovits A. R., Luedemann G., Mello T. R. B., Pinto A. S., Munhoz C. B. R. & Takahashi F. S. C. (2012) Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). *Plant Ecol*. **213**, 795–808.

Carvalho G. H. & Batalha M. A. (2013) The drivers of woody species richness and density in a Neotropical savannah. *Biol Lett*. **9**, 20130412.

Carvalho G. H., Batalha M. A., Silva I. A., Cianciaruso M. V. & Petchey O. L. (2014) Are fire, soil fertility and toxicity, water availability, plant functional diversity, and litter decomposition related in a Neotropical savanna? *Oecologia* **175,** 923-935.

Castro E. A. & Kauffman J. B. (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *J Trop Ecol* **14,** 263-283.

Cianciaruso M. V., Silva I. A. & Batalha M. A. (2010) Aboveground biomass of functional groups in the ground layer of savannas under different fire frequencies. *Aust J Bot* **58**, 169–174.

Cianciaruso M. V., Silva I. A., Batalha M. A., Gaston K. J. & Petchey O. L. (2012) The influence of fire on phylogenetic and functional structure of woody savannas: moving from species to individuals. *Perspect Plant Ecol Evol Syst* **14**, 205–216.

Coutinho L. M. (1990) *Fire in the ecology of the Brazilian cerrado*. In: Fire in the tropical biota (ed J. C. Goldammer) pp. 81–103. Springer, Berlin.

Delhaize E. & Ryan P. R. (1995) Aluminum Toxicity and Tolerance in Plants. *Plant Physiol* **107,** 315-321.

Di Iorio A., Montagnoli A., Scippa G. S. & Chiatante D. (2011) Fine root growth of *Quercus pubescens* seedlings after drought stress and fire disturbance. *Environ Exp Bot* **74,** 272-279.

Díaz S., Lavorel S., de Bello F., Quétier F., Grigulis K. & Robson T. M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *P Natl Acad Sci* **104**, 20684–20689.

February E. C., Cook G. D. & Richards A. E. (2013) Root dynamics influence tree-grass coexistence in an Australian savanna. *Austral Ecol*. **38**, 66–75.

Fierer N. & Jackson R. B. (2006) The diversity and biogeography of soil bacterial communities. *P Natl Acad Sci* **103**, 626–631.

Fitter A. H. (1987) An architectural approach to the comparative ecology of plant root systems. *New Phytol.* **106,** 61–77.

Forde B. & Lorenzo H. (2001) The nutritional control of root development. *Plant Soil* **232,** 51-68.

França H., Ramos-Neto M. B. & Setzer, A. (2007) *O fogo no Parque Nacional das Emas*. Ministério do Meio Ambiente, Brasília.

Gignoux J., Clobert J. & Menaut, J. C. (1997) Alternative fire resistance strategiesin savanna trees. *Oecologia*. **110**, 576–583.

Gill R. A. & Jackson, R. B. (2000) Global patterns of root turnover for terrestrial ecosystems.

New Phytol **147,** 13-31.

Goodland R. (1971) A Physiognomic Analysis of the `Cerrado' Vegetation of Central Brasil. *J Ecol* **59**, 411–419.

Gottsberger G. & Silberbauer-Gottsberger, I. (2006) *Life in the cerrado: a South American tropical seasonal vegetation*. Reta, Ulm.

Grace J. B. (2007) Does species diversity limit productivity in natural grassland communities? *Ecol Lett* **10,** 680-689.

Grime J. P. (1979) *Plant strategies, vegetation processes and ecosystem properties*. 2nd Ed. John Wiley & Sons, West Sussex.

Grime J.P., Crick J.C. & Rincon J.E. (1986) The ecological significance of plasticity. *Symp. Soc. Exp. Biol.* **40,** 5–29.

Hoffmann W. A., Adasme R., Haridasan M., Carvalho M. T., Geiger E. L., Pereira M. A. B., Gotsch S. G. & Franco A. C. (2009) Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology*. **90**, 1326–1337.

Jackson P. C., Meinzer F. C., Bustamante M., Goldstein G., Franco A., Rundel P. W., Caldas L., Igler E. & Causin F. (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiol* **19,** 717-724.

Jackson R. B., Canadell J., Ehleringer J. R., Mooney H. A., Sala O. E. & Schulze E. D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* **108,** 389-411.

Jackson R. B., Mooney H. A. & Schulze E. D. (1997) A global budget for fine root biomass, surface area, and nutrient contents. *P Natl Acad Sci* **94**, 7362–7366.

Jensen M., Michelsen A. & Gashaw M. (2001) Responses in plant, soil inorganic and microbial nutrient pools to experimental fire, ash and biomass addition in a woodland savanna. *Oecologia* **128**, 85–93.

Keddy P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *J Veg Sci* **3,** 157-164.

Kochian L. V. (1995) Cellular mechanisms of aluminum toxicity and resistance in plants. *Annu Rev Plant Physiol Plant Mol Biol* **46,** 237-260.

Köppen W. (1931) *Grundriss der Klimakunde*. Gruyter, Berlin.

Krebs C. J. (1998) *Ecological methodology*. Harper Collins, New York.

Ladwig L. M., Collins S. L., Swann A. L., Xia Y., Allen M. F. & Allen E. B. (2012) Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia*. **169**, 177–185.

Lei P., Scherer-Lorenzen M. & Bauhus J. (2012) The effect of tree species diversity on fine-root production in a young temperate forest. *Oecologia*. **169**, 1105–1115.

Loreau M. & Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* **412,** 72-76.

Malamy J. E. (2005) Intrinsic and environmental response pathways that regulate root system architecture. *Plant Cell Environ* **28**, 67–77.

Mokany K., Raison R. J. & Prokushkin A. S. (2006) Critical analysis of root : shoot ratios in terrestrial biomes. *Glob Change Biol* **12**, 84–96.

Oliveira R. S., Bezerra L., Davidson E. A., Pinto F., Klink C. A., Nepstad D. C. & Moreira A. (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Funct Ecol* **19**, 574–581.

Oliveira-Filho A. T. & Ratter, J. A. (2002) *Vegetation physiognomies and woody flora of the Cerrado Biome.* In: The Cerrados of Brazil: ecology and natural history of a Neotropical savanna (eds P. S. Oliveira & R. J. Marquis) pp. 91–120 Columbia University Press, New York.

Paula S. & Pausas, J. G. (2011) Root traits explain different foraging strategies between resprouting life histories. *Oecologia*. **165**, 321–331.

Pausas J. G., Bradstock R. A., Keith D. A., Keeley J. E. & GCTE (Global Change of Terrestrial Ecosystems) (2004) Plant functional traits in relation to fire and crown-fire ecosystems. *Ecology*. **85**, 1085–1100.

Pausas J. G. & Keeley, J. E. (2009) A Burning Story: The Role of Fire in the History of Life. *BioScience*. **59**, 593–601.

Pärtel M., Hiiesalu I., Öpik M. & Wilson S. D. (2012) Below-ground plant species richness: new insights from DNA-based methods. *Funct Ecol*. **26**, 775–782.

Price J. N., Hiiesalu I., Gerhold P. & Pärtel M. (2012) Small-scale grassland assembly patterns differ above and below the soil surface. *Ecology*. **93**, 1290–1296.

R Core Team (2013) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna. URL: http://www.R-project.org/.

Raij B., Quaggio J. A., Cantarella H., Ferreira M. E., Lopes A. S. & Bataglia O. C. (1987) *Análise química de solos para fins de fertilidade*. Fundação Cargill, Campinas.

Ribeiro S. C., Fehrmann L., Soares C. P. B., Jacovine L. A. G., Kleinn C., Gaspar, R. O. (2011) Above- and belowground biomass in a Brazilian Cerrado. *Forest Ecol Manag*. **262**, 491–499.

Rodríguez A., Durán J., Fernández-Palacios J. M., Gallardo A. (2009) Short-term wildfire effects on the spatial pattern and scale of labile organic-N and inorganic-N and P pools. *Forest Ecol Manag*. **257**, 739–746.

Rossatto D. R., Silva L. C. R., Villalobos-Vega R., Sternberg L. D. S. L. & Franco A. C. (2012) Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. *Environ Exp Bot* **77,** 259-266.

Rosseel Y. (2012) Lavaan: An R package for structural equation modeling. *J. Stat. Soft.* **48,** 1–36. URL: http://www.jstatsoft.org/v48/i02/.

Scholes R. J. & Archer S. R. (1997) Tree-grass interactions in Savannas. *Ann Rev Ecol Syst* **28,** 517-544.

Silva D. M. & Batalha M. A. (2008) Soil–vegetation relationships in cerrados under different fire frequencies. *Plant Soil*. **311**, 87–96.

Srivastava D. S. & Vellend M. (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* **36**, 267–294.

Stubbs W. J. & Wilson J. B. (2004) Evidence for limiting similarity in a sand dune community. *J Ecol* **92,** 557-567.

Tateno R., Hishi T. & Takeda H. (2004) Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. *Forest Ecol Manag* **193**, 297–306.

Tilman D., Lehman C. L. & Thomson K. T. (1997) Plant diversity and ecosystem productivity: theoretical considerations. *P Natl Acad Sci* **94**, 1857–1861.

Verdaguer D. & Ojeda F. (2002) Root rtarch storage and allocation patterns in seeder and resprouter seedlings of two Cape *Erica* (Ericaceae) species. *Am J Bot.* **89**, 1189–1196.

Whiting S. N., Leake J. R., McGrath S. P. & Baker A. J. M. (2000) Positive responses to Zn and Cd by roots of the Zn and Cd hyperaccumulator *Thlaspi caerulescens*. *New Phytol* **145,** 199-210.

Yachi S. & Loreau M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *P Natl Acad Sci* **96**, 1463–1468.

Zwicke M., Alessio G. A., Thiery L., Falcimagne R., Baumont R., Rossignol N., Soussana J. F., & Picon-Cochard C. (2013) Lasting effects of climate disturbance on perennial grassland above-ground biomass production under two cutting frequencies. *Glob Change Biol* **19,** 3435-3448.

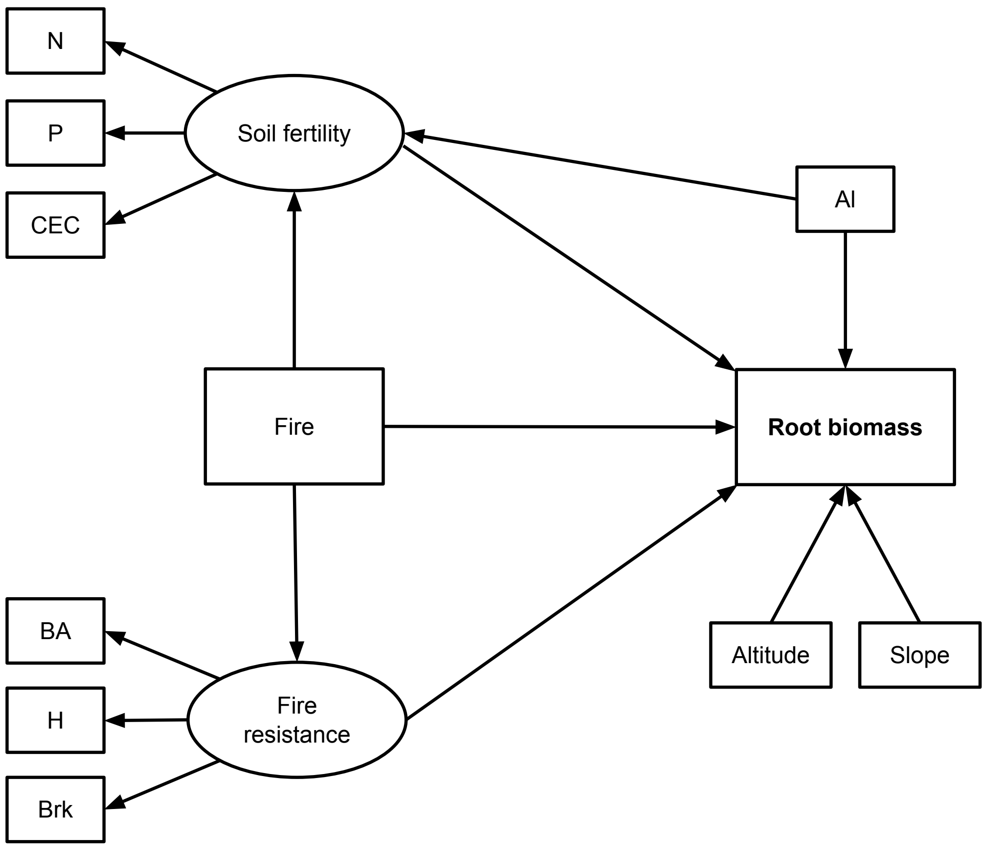

Fig. 1 - A priori casual model relating soil fertility, topographic variables, fire intensity, and fire resistance to fine and coarse root biomass in cerrado. We considered soil fertility a latent variable causing nitrogen (N) and phosphorus (P) content, and cation exchange capacity (CEC, mmol kg^{-1}); fire resistance causing basal area (BA, m^2), height (H, m), and bark thickness (Brk, mm). Recent fire is the penultimate fire that occur 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).

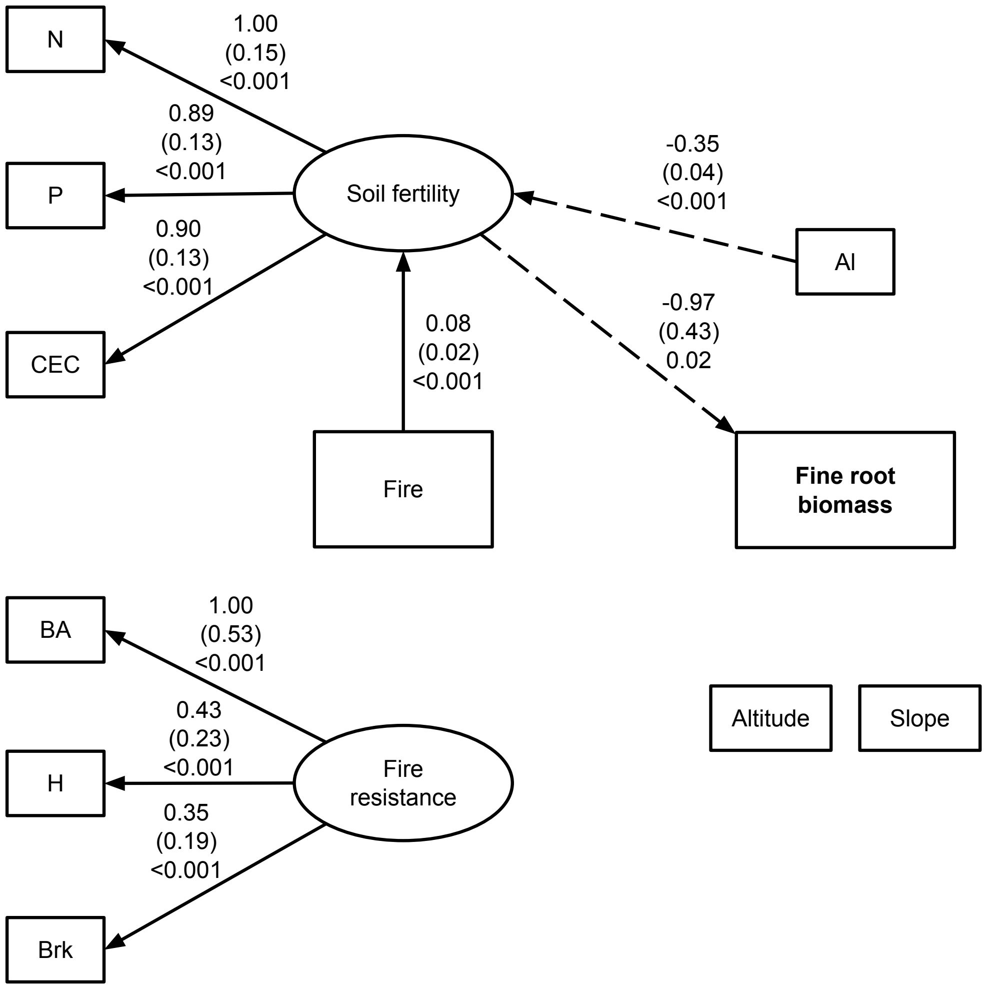

Fig. 2 - Final model predicting fine deep root biomass, with less than 2 mm diameter sampled from 20 to 100 cm deep in the soil, with best fit to the data (χ^2 = 50.58, d.f. = 35, P = 0.04). Unstandardised estimates, standardised estimates between parenthesis, and P values of each relationships. Solid arrows indicate significant and positive paths; dashed arrows indicate significant and negative paths; non-significant paths were omitted.

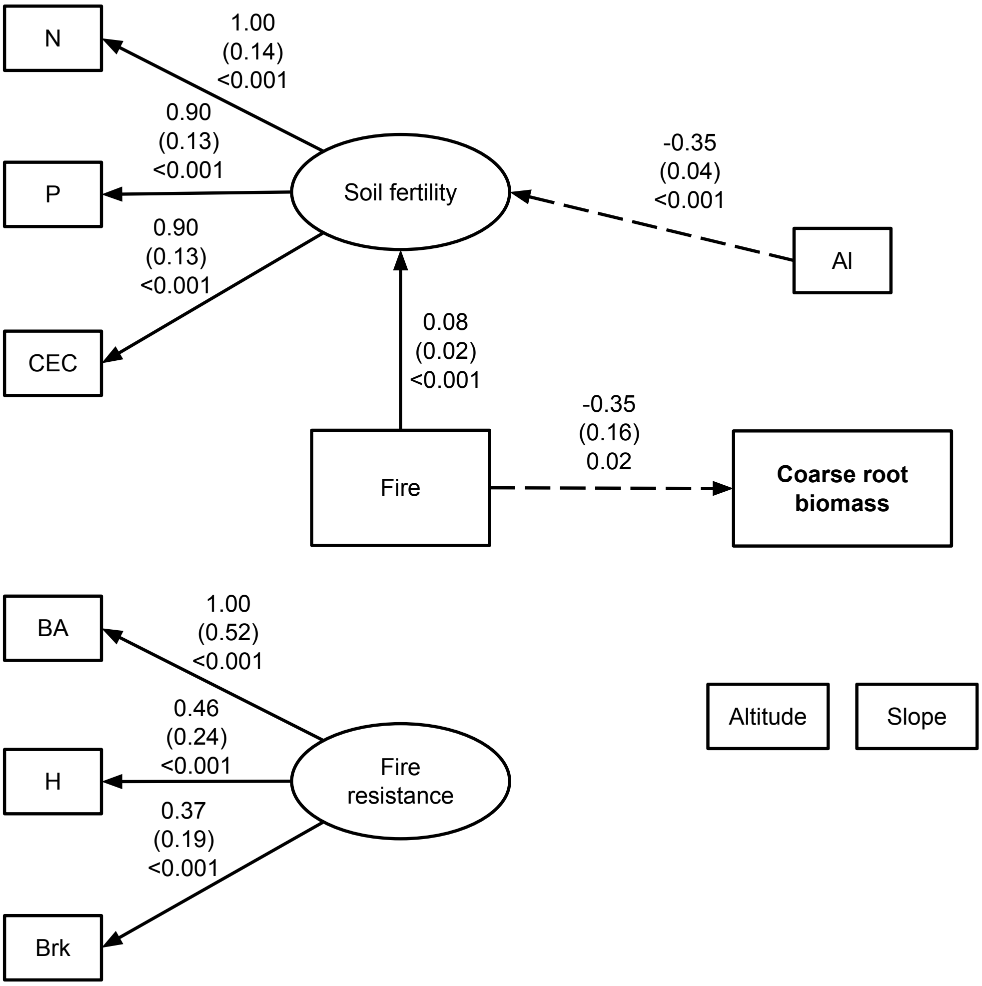

Fig. 3 - Final model predicting coarse deep root biomass, with 2 mm diameter or more and sampled from 20 to 100 cm deep in the soil, with best fit to the data (χ^2 = 44.71, d.f. = 35, P = 0.12). Unstandardised estimates, standardised estimates between parenthesis, and P values of each relationships. Solid arrows indicate significant and positive paths; dashed arrows indicate significant and negative paths; non-significant paths were omitted.

V - CONCLUSÃO GERAL

CONCLUSÃO GERAL

Neste trabalho, vimos que a biomassa hipógea é um componente importante do estoque de carbono no cerrado. A diversidade de espécies e a divergência funcional estiveram positivamente relacionadas com a biomassa epígea das árvores, mas não com a biomassa hipógea. Diferenças nas medidas de divergência funcional sugerem a existência de mecanismos que limitam a similaridade entre as espécies das comunidades. Comunidades mais divergentes devem ter maior complementaridade no uso dos recursos, levando a uma maior biomassa epígea. No entanto, nenhum dos índices de diversidade tiveram relação com a biomassa das raízes do cerrado ou da floresta estacional semidecidual. As medidas de diversidade obtidas acima do nível do solo não foram boas preditoras do estoque total de carbono das comunidades vegetais, pois não previram a biomassa hipógea dessas comunidades.

Dessa forma, o uso de variáveis ambientais e traços funcionais foi imprescindível para prevermos o estoque subterrâneo de carbono. Usamos variáveis relacionadas à qualidade nutricional do solo, variáveis topográficas e medidas de frequência de fogo nas parcelas, além da média e variação dos traços funcionais das espécies, e geramos modelos que previram a biomassa e produtividade hipógeas no cerrado e na floresta estacional semidecidual. Os modelos foram significativos, apesar de terem baixo poder explicativo no cerrado. Nossos modelos mostraram que comunidades com menos distúrbios, melhor qualidade de solo, e maior acesso à água foram mais produtivas, sugerindo que elas são controladas por interações entre disponibilidade de nutrientes e água. Ao contrário do que esperávamos, a frequência de fogo não afetou a biomassa hipógea no cerrado, possivelmente por uma estabilidade funcional das comunidades, fazendo com que as espécies tenham estratégias similares de crescimento de raíz. Além disso, maior divergência de traços funcionais nas parcelas de cerrado, mas não na floresta estacional, levou a um aumento na biomassa hipógea, sugerindo diferenciação de nicho e maior complementaridade entre os traços funcionais das espécies. Menor intensidade de distúrbio, forrageamento por potássio no cerrado e nitrogênio na floresta, e maior complementaridade entre as espécies no cerrado foram os processos ecológicos que afetaram a biomassa total e produtividade hipógeas no cerrado e na floresta estacional semidecidual.

Dividimos a biomassa hipógea do cerrado em raízes finas e grossas e separamos os horizontes superficial e profundo, para entendermos como a disponibilidade de recursos e os distúrbios afetam a biomassa destes componentes. Identificamos a fertilidade do solo causando menor biomassa de raízes finas e fogos recentes causando menor biomassa de raízes grossas, abaixo de 20 cm de profundidade no solo. A biomassa de raízes superficiais não está relacionada a nenhum dos processos ecológicos estudados, e deve ser causada por interações bióticas entre as espécies, como facilitação ou competição.

Diferente do que esperávamos, a baixa disponibilidade de cátions no solo levou as espécies a investirem mais em raízes finas, aumentando a captação dos nutrientes, e permitindo a sobrevivência em solos pobres. Esperávamos que o fogo causasse aumento na biomassa de raízes grossas, devido a um maior investimento das espécies vegetais em órgãos de armazenamento subterrâneos usados para rebrotar. No entanto, as queimadas recentes pareceram substituir a composição das espécies das comunidades, levando à maior proporção de espécies do componente herbáceo-subarbustivo, que possuem menor biomassa de raízes grossas. As biomassas hipógeas do cerrado e da floresta estacional semidecidual não puderam ser previstas pela diversidade de espécies ou pela diversidade funcional das parcelas, mas estiveram relacionadas com variáveis ambientais e traços funcionais das espécies arbóreas, e esses efeitos foram diferentes sobre a biomassa das raízes finas e grossas.