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Do woody and herbaceous species compete for soil water across topographic gradients? Evidence for niche partitioning in a Neotropical savanna

D.R. Rossatto [a,*], L.C.R. Silva [b], L.S.L. Sternberg [c], A.C. Franco [d]

[a] Departamento de Biologia Aplicada, FCAV, Universidade Estadual Paulista "Júlio de Mesquita Filho", Via de Acesso Prof. Paulo Donato Castellane s/n, CEP 14884-900 Jaboticabal, SP, Brazil
[b] Department of Land, Air and Water Resources, University of California, Davis, CA 95616, USA
[c] Department of Biology, University of Miami, Coral Gables, FL 33124, USA
[d] Departamento de Botânica, Universidade de Brasília, Caixa Postal 04457, Brasília, DF 70904-970, Brazil

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ABSTRACT

Savannas are characterized by sparsely distributed woody species within a continuous herbaceous cover, composed mainly by grasses and small eudicot herbs. This vegetation structure is variable across the landscape, with shifts from open grassland to savanna woodland determined by factors that control tree density. These shifts often appear coupled with environmental variations, such as topographic gradients. Here we investigated whether herbaceous and woody savanna species differ in their use of soil water along a topographic gradient of about 110 m, spanning several vegetation physiognomies generally associated with Neotropical savannas. We measured the δ^2H and δ^{18}O signatures of plants, soils, groundwater and rainfall, determining the depth of plant water uptake and examining variations in water uptake patterns along the gradient. We found that woody species use water from deeper soil layers compared to herbaceous species, regardless of their position in the topographic gradient. However, the presence of a shallow water table restricted plant water uptake to the superficial soil layers at lower portions of the gradient. We confirmed that woody and herbaceous species are plastic with respect to their water use strategy, which determines niche partitioning across topographic gradients. Abiotic factors such as groundwater level, affect water uptake patterns independently of plant growth form, reinforcing vegetation gradients by exerting divergent selective pressures across topographic gradients.

1. Introduction

The use of resources by plants is of fundamental importance to understand ecological processes in natural landscapes (Ferreira et al., 2007; Higgins et al., 2011), particularly those associated with the maintenance of species diversity (Mckane et al., 2002) and multiple patterns of vegetation structure and function (Grime, 2001). A series of recent studies have related the partitioning of essential resources, such as nutrients and water, with plant species diversity and co-existence of contrasting life-forms (Désilets and Houle, 2005; Saha et al., 2009; Staver et al., 2011; Verweij et al., 2011; Hold, 2013). Resource use and niche partitioning appear to be especially relevant in vegetation physiognomies where a large number of species occur side by side and where environmental filters (e.g. abiotic constraints) shape vegetation structure, composition and function (Higgins et al., 2011; Sales et al., 2013).

The Neotropical savannas of Brazil (regionally called "Cerrado") are characterized by contrasting environmental conditions, where strong seasonality, high evaporative demand, low soil nutrient availability and frequent fire events explain the long-term persistence of vegetation mosaics (Eiten, 1972; Gottsberger and Silberbauer-Gottsberger, 2006; Silva et al., 2013). As in many other tropical regions, natural landscapes of central Brazil comprise a wide range of vegetation physiognomies, ranging from open grasslands to savanna woodlands, readily identifiable by shifts in the proportion of woody plants, which may occur densely or sparsely distributed within a continuous herbaceous matrix composed mainly by eudicots herbs and grasses (Oliveira-Filho and Ratter, 2002). The variability in physiognomic types often appears along shallow topographic gradients, where a mosaic of plant communities co-exists as a consequence of the wide range of interactions between water flow, soil properties, nutrients and fire frequency that change even with small differences in topography (Oliveira-Filho et al., 1989; Rossatto et al., 2012). In these gradients, vegetation structure and species composition vary greatly across the landscape, and structural changes tend to follow diversity patterns of woody and herbaceous species distribution (Oliveira-Filho and Ratter, 2002). In the upper portions of the gradient, characterized by deep oxysols, dense woody savannas are the most common vegetation type (Silberbauer-Gottsberger and Eiten, 1987). The density of woody species decreases as soils become shallower towards lower elevations, where more open shrubby savanna formations with a few trees and richer eudicots herbaceous communities appear, and eventually give place to wet grasslands

* Corresponding author. Tel.: +55 16 3209 7190.
E-mail address: drrossatto@gmail.com (D.R. Rossatto).

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at the lowest elevations near riparian zones and seasonally flooded soils (Eiten, 1972; Silberbauer-Gottsberger and Eiten, 1987; Furley, 1999).

Variations in density of woody species in Neotropical savannas have long been thought to represent the result of competition for resources with herbaceous species (Eiten, 1972; Medina and Silva, 1990). Alternatively, changes in soil properties and groundwater depth (Oliveira-Filho et al., 1989; Villalobos-Vega, 2010; Rossatto et al., 2012) combined with fire frequency (Oliveira-Filho and Ratter, 2002) and nutrient limitation (Silva et al., 2013), could explain the persistence of contrasting vegetation forms. Water availability is considered to be one of the most important factors constraining woody cover in savannas (Sankaran et al., 2005), but this has not been tested separately from other environmental filters (i.e. nutrient limitation and fire frequency), limiting predictions of vegetation shifts based on water regime alone. It is well known that the water niche partitioning plays an important role in the co-existence of diverse plant species in a wide variety of vegetation types (Walter, 1971; Nippert and Knapp, 2007; Eggemeyer et al., 2008; Ward et al., 2013). This potential mechanism of co-existence has been extensively explored in natural systems dominated by tree species (Schenk and Jackson, 2002; Verweij et al., 2011) or to explain tree–grass co-dominance in dry savannas (Hold, 2013; Ward et al., 2013), however whether similar mechanism could explain the co-existence of trees and diverse communities of eudicot herbs as typical of mesic and humid Neotropical savannas are yet to be determined (Rossatto et al., 2013).

Here we test whether woody and herbaceous eudicot plants compete for water resources across a topographic gradient consisting of distinct vegetation physiognomies typical of Neotropical savannas. The estimation of the depth of plant water uptake was based on comparisons of oxygen isotope ratios of plant stem water and soil pore water collected at different depths (Dawson et al., 2002). Nutritional and fire pressures are similar across the gradient and water depth is considered the main driver of vegetation change at the study site. We expect to find that the preferential depth of water uptake will differ between woody and herbaceous communities only in upper slope vegetation, where groundwater level is deeper (Rossatto et al., 2012; Rossatto et al., 2013) and woody species, which typically have better developed root systems (Oliveira et al., 2005), will be able to exploit deeper layers of the soil profile. As a result, we expect to demonstrate that competition for water is stronger in lower elevation plant communities, where groundwater depth decreases (Rossatto et al., 2012) and the exploitable soil layers reduced in comparison with upper slope vegetation.

2. Materials and methods

2.1. Study area and species selection

Our study was performed at the IBGE Ecological Reserve, located 33 km south of Brasília, Distrito Federal, in Brazil (15°56′S, 47°53′W). The IBGE reserve is located at an average altitude of 1100 m above the sea level, showing gentle topographic gradients and encompassing several natural vegetation physiognomies. The average annual rainfall in the region is approximately 1500 mm, with a pronounced dry season from May through September. Mean monthly temperatures range from 19 to 23 °C. At the study site it is possible to find deep and well-drained oxysols, but cambisols and hydromorphic (seasonally flooded) soils also occur associated with hill slopes and valley bottoms, respectively (Scholz et al., 2008).

To study the variation on depth of water uptake of woody and herbaceous eudicots plants we employed a transect of 1500 m spanning an elevation gradient of about 110 m. This transect covered several typical vegetation physiognomies generally associated with savannas in the regions; namely, open grasslands to woodlands (Furley, 1996, 1999). Following changes in vegetation structure and composition (Rossatto et al., 2012), we subdivided the transect in 5 segments from the highest to the lowest elevation (Fig. S1 — Supplementary Material). The two first segments of the transect (A and B) supported typical savanna vegetation, regionally called cerrado sensu stricto (a matrix of co-existing woody, herbaceous eudicots and grasses species, with high tree density). The following segments (C and D) were covered by a more open shrub-dominated savanna, regionally called *campo cerrado*, while the last segment (E) consisted of a very open (nearly treeless) physiognomy, regionally called *campo sujo* (for details consult Table S1 in Supplementary Data).

In each of the studied segments we selected 7 woody species, here defined as plants with a distinct single, lignified main stem, generally taller than 2 m; and 6–7 herbaceous species, here defined as small eudicot plants of approximately 10–30 cm in height, with or without a small non-ramified stem partially lignified. (See species at Table S2 at Supplementary Data). All selected plants were sampled using the methods described below.

2.2. Defining plant water source

We determined the oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) signatures of the plant stem, soil samples, groundwater and rainfall. The depth of water uptake of woody and herbaceous stratum was estimated by matching the $\delta^{18}O$ of stem water with $\delta^{18}O$ signatures of soil profiles. In this way we compared woody and herbaceous communities' isotopic signatures in terms of deep (more negative values in $\delta^{18}O$ signatures) or superficial (less negative values in $\delta^{18}O$ signatures) water uptake. Similar methodology has been previously applied elsewhere (e.g. Jackson et al., 1999; Meinzer et al., 1999; Querejeta et al., 2007). Values of $\delta^{2}H$ stem signatures were used to verify if samples were near or far from the meteoric water line.

Stem samples of woody and herbaceous species, one individual per species, were collected at each of the five plots. Tree and herb stem samples of about 3 cm in diameter had the bark stripped off and cut into pieces of 10 cm length, which were sealed in glass tubes to prevent evaporation and immediately refrigerated in an insulated container. Samples were collected from adult individuals in November 2007 during the wet season, after a period of two weeks without rainfall. Soil samples were collected at each of the five sampling areas to determine variations of $\delta^{18}O$ signatures at different depths of the soil profile. Soil samples were collected at the top 0–10-cm depth and then at intervals of 20 cm down to 1.9 meters depth (in the highest portions of the gradient) or until the groundwater was reached (in the lowest part of the gradient). We used previously published data for soil samples, groundwater level at each site and the meteoric water line of the region of the study (Rossatto et al., 2012) to infer plant water source.

The water extraction from plant stems and soils was conducted at the Plant Physiology Laboratory of the University of Brasília, following the methodology proposed by Vendramini and Sternberg (2007). Water extracted from the soil and stem samples were sealed in glass tubes and sent to the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (Department of Biology, University of Miami, Miami, Florida). Water samples were analyzed in a Multiflow system connected to an Isoprime mass spectrometer (Elementar, Hanau, Germany). Oxygen and hydrogen isotope ratios are reported here as $\delta^{18}O$ and $\delta^{2}H$ values respectively and calculated as:

$$\delta^{18}O \quad \text{or} \quad \delta^{2}H = \left\{\left(R_{sample}/R_{SMOW}\right)-1\right\} \times 1000$$

where R_{sample} and R_{SMOW} represent the heavy to light isotope ratio of the sample and the standard respectively. The standard for water isotope ratios used here was Vienna standard mean ocean water (SMOW) and the precision of the analysis was ±0.1‰ and ±2.0‰ for oxygen and hydrogen isotopes respectively.