



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



D.R. Rossatto <sup>a,\*</sup>, L.C.R. Silva <sup>b</sup>, L.S.L. Sternberg <sup>c</sup>, A.C. Franco <sup>d</sup>

<sup>a</sup> 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

<sup>b</sup> Department of Land, Air and Water Resources, University of California, Davis, CA 95616, USA

<sup>c</sup> Department of Biology, University of Miami, Coral Gables, FL 33124, USA

<sup>d</sup> Departamento de Botânica, Universidade de Brasília, Caixa Postal 04457, Brasília, DF 70904-970, Brazil

## ARTICLE INFO

### Article history:

Received 13 July 2013

Received in revised form 10 November 2013

Accepted 14 November 2013

Available online 14 December 2013

Edited by RM Cowling

### Keywords:

Cerrado  
Growth forms  
Herbaceous layer  
Niche partitioning  
Resource use  
Water uptake  
Woody layer

## 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  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  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.

© 2013 SAAB. Published by Elsevier B.V. All rights reserved.

## 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 eudicot 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 oxisols, 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 eudicot herbaceous communities appear, and eventually give place to wet grasslands

\* Corresponding author. Tel.: +55 16 3209 7190.

E-mail address: [drrossatto@gmail.com](mailto:drrossatto@gmail.com) (D.R. Rossatto).

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; Eggemeier 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 oxisols, 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 eudicot 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 ( $\delta^{18}\text{O}$ ) and hydrogen ( $\delta^2\text{H}$ ) 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  $\delta^{18}\text{O}$  of stem water with  $\delta^{18}\text{O}$  signatures of soil profiles. In this way we compared woody and herbaceous communities' isotopic signatures in terms of deep (more negative values in  $\delta^{18}\text{O}$  signatures) or superficial (less negative values in  $\delta^{18}\text{O}$  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  $\delta^2\text{H}$  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  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  values respectively and calculated as:

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

where  $R_{\text{sample}}$  and  $R_{\text{SMOW}}$  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  $\pm 0.1\%$  and  $\pm 2.0\%$  for oxygen and hydrogen isotopes respectively.

### 2.3. Statistical analysis

We compared the average values of plant stem isotope water signature ( $\delta^{18}\text{O}$ ) through a factorial ANOVA, aiming to test the effects of dominant growth form of each plant community (woody vs. herbaceous) and the position on topographic gradient (points A, B, C, D and E) in the depth of water uptake. The factorial ANOVA was followed by Tukey's test ( $\alpha = 0.05$ ) when the factors were proved to be significant. The relationship between  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  for soils, rainfall and stem water from the different growth forms were analyzed using simple linear regression. All data presented normality ( $P > 0.66$  according to the Kolmogorov–Smirnov test) and homogeneity of variances, according to the Levene's test ( $F_{1,52} = 0.35$   $P = 0.66$ ).

## 3. Results

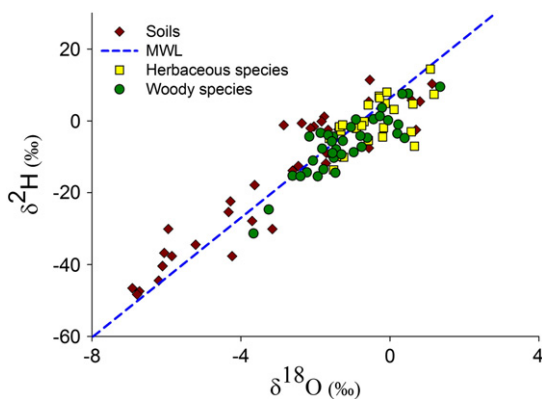
### 3.1. Rainfall, soil and groundwater isotopic composition

In Fig. 1 a plot of  $\delta^2\text{H}$  versus the  $\delta^{18}\text{O}$  values of rainfall water is presented. This relationship is described as a line with slope of 8.3 and intercept of 6.33, which is very similar to that found for the global meteoric water line (GMWL,  $\delta^2\text{H} = 8\delta^{18}\text{O} + 10$ ). The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values obtained from soil and plant water samples also fell near the global meteoric water line (Fig. 1).

In all studied vegetation types we found significant changes in isotopic signatures with soil depth (Fig. 2A–E). In all cases, the soil water  $\delta^{18}\text{O}$  from the superficial (0–50 cm) layers of the profile was enriched (between 0 and  $-2\text{‰}$ ) compared to that found in the deeper layers, whose soil water  $\delta^{18}\text{O}$  values tended to be similar to or more negative than the groundwater signature (Fig. 2). Soil profiles from upper slope segments had the most pronounced variations in isotopic composition, while at down slope segments of the transect (especially locations D and E), the oxygen isotopic composition along the soil profile did not vary significantly (Fig. 2).

### 3.2. The effect of topographic position and growth forms on isotopic signatures

There was a significant effect of growth form ( $F_{1,52} = 6.38$   $P < 0.001$ ) and of topographic position ( $F_{4,52} = 2.12$   $P = 0.048$ ) in the  $\delta^{18}\text{O}$  values of plant stem (Fig. 3A–B). Interactions between topographic position and growth form were not significant ( $F_{4,52} = 0.79$   $P = 0.467$ ), with  $\delta^{18}\text{O}$  of stem water being always more negative in upper slope ( $-1.47 \pm 0.29\text{‰}$ ) than down slope ( $-0.64 \pm 0.24\text{‰}$ ) (Tukey's test  $P < 0.05$ ), regardless of changes in vegetation structure. The same was found when comparing woody ( $-1.12 \pm 0.17\text{‰}$ ) and herbaceous ( $-0.47 \pm 0.16\text{‰}$ ) species (Tukey's test  $P < 0.01$ ), with



**Fig. 1.** The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  signatures of soils and  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  signatures of plant stem water for herbaceous and woody species collected at different positions along the topographic gradient. Regression line for meteoric water line (MWL):  $\delta^2\text{H} = 8.3\delta^{18}\text{O} + 6.33$ ,  $r^2 = 0.993$   $P < 0.01$ . Data for soil samples retrieved from Rossatto et al. (2012).

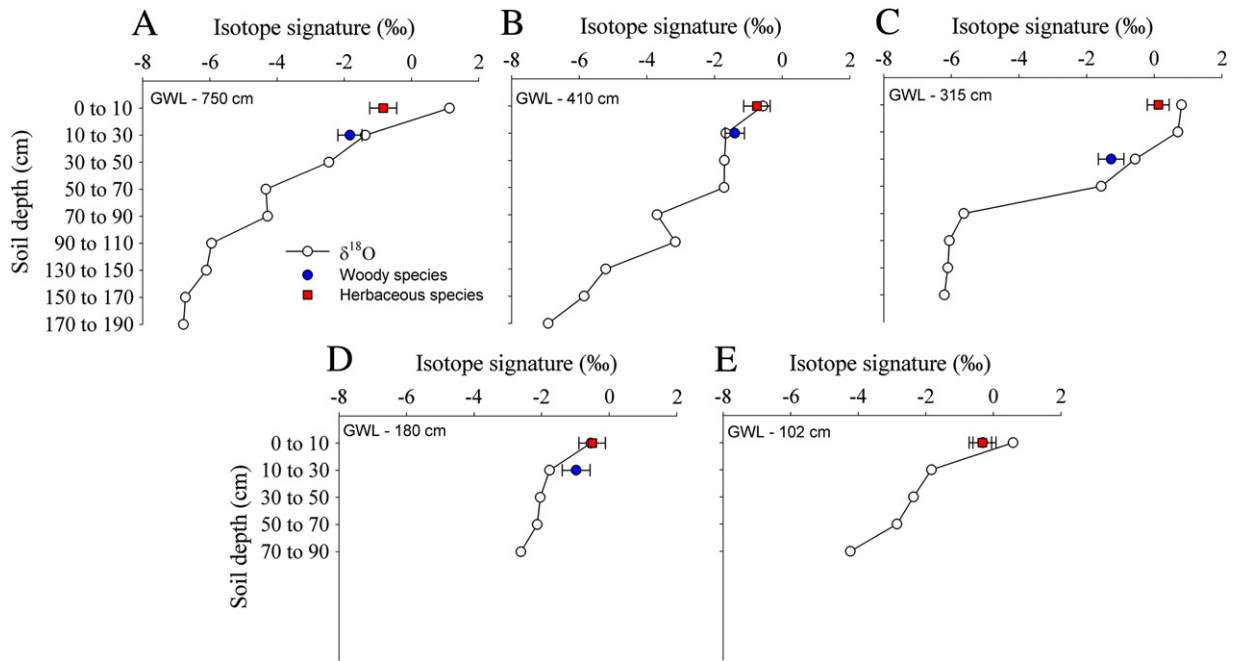
the average values of  $\delta^{18}\text{O}$  ‰ for woody and herbaceous communities (Fig. 2) showing that herbaceous community tended to have  $\delta^{18}\text{O}$  signatures that match superficial soil layers (0–30 cm), while woody species showed signatures matching deeper soil layers (10–50 cm). The exception was in the lowest slope position of the topographic gradient (Fig. 2E), where  $\delta^{18}\text{O}$  signatures were similar in woody and herbaceous plants communities, showing that all studied plants acquired water predominantly from the superficial soil layers (0–30 cm).

## 4. Discussion

We confirmed our hypothesis that woody and herbaceous species have intrinsically different water uptake strategies, representing a resource-driven niche partitioning. Resource partitioning belowground among life-forms are consistent with previous observations in mesic savannas (Rossatto et al., 2013) and temperate grasslands (Dodd et al., 1998; Nippert and Knapp, 2007). Here we extend these observations by showing that partitioning of soil water resources by woody and herbaceous plants is maintained along topographical gradients. These differences in patterns of water uptake, with trees extracting water from deeper soil layers in comparison with herbs, were consistent along the different savanna physiognomies across the topographic gradient. The only significant deviation from this general trend was the lowest slope position, where the depth of water uptake in both groups was constrained to superficial soils (0–30 cm) by shallow groundwater levels.

Woody communities from higher slope segments of the transect, where we found a deep water table ( $\sim 7$  m depth) (Fig. 2A–B), appear to rely mostly on water from relatively deeper soil layers ( $>0.50$  cm), whereas water uptake in herbaceous communities at those same high elevations relied on superficial soil water ( $<0.40$  cm). It is important to note that these observations were made after two weeks without rainfall under warm conditions, suggesting that soil water extraction in herbaceous species may be restricted to shallower soil layers by root development. Many previous studies have shown that trees in savannas normally extract water from deeper layers of the soil profile (Dodd et al., 1998; Verweij et al., 2011; Yang et al., 2011; Rossatto et al., 2013; Hold, 2013; Ward et al., 2003), however few studies were able to compare differences in water uptake between woody and eudicot herbaceous plants (Rossatto et al., 2013). While savanna woody plants are plastic with respect to preferential water uptake, varying from shallow to deep soil sources according to small changes in topography, eudicot herbs are much less plastic and are restricted to the superficial soil layers throughout the topographic gradient. Furthermore, our results suggest that competition for water between woody and herbaceous species is maximized at low slope positions. Even though water appears to be readily available in those segments, high groundwater levels lead to anoxic conditions in deeper soil layers, confining root distribution of all species to shallow soil layers (Fig. 3E). Along with our results, a broader observation of landscape patterns in the region, indicates that under such (shallow soils) conditions woody plants are outcompeted by herbaceous species, while the reverse would be expected in upland systems.

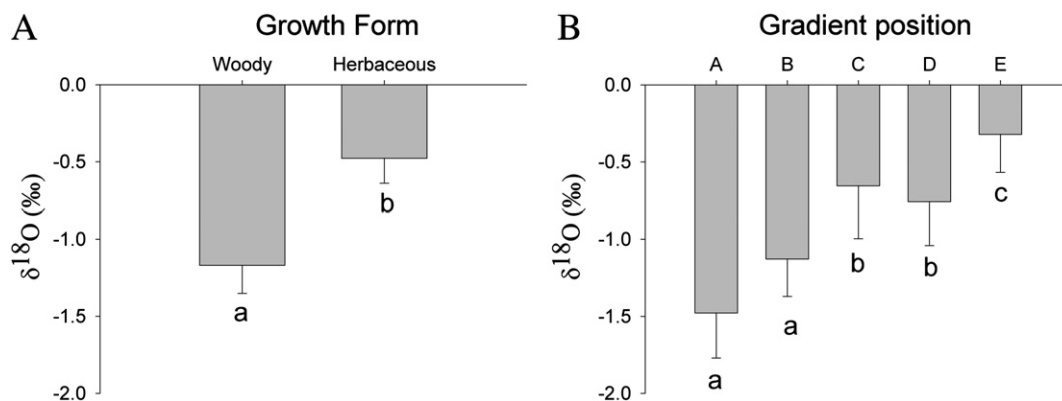
The greater availability of unsaturated soil in the upper portion of the topographic gradient implies a much larger available soil volume for root growth than at lower portions of the gradient (Fig. 2), which may also be connected with critical differences in nutrient availability, explaining why in such topographic positions woody species predominate (Rossatto et al., 2012). The amplitude of water niches to be exploited is higher in uplands than in seasonally flooded lowlands (Araya et al., 2010). In turn, this supports more structurally and compositionally diverse communities, offering a mechanism to explain the co-existence of multiple vegetation physiognomies in water-limited systems of the seasonal tropics (Eggemeier et al., 2008; Yang et al., 2011; Araya et al., 2010).



**Fig. 2.** Soil water (black lines with white dots) and averages of the woody (dot) and herbaceous (square) community plant stem water signatures for  $\delta^{18}\text{O}$  of different physiognomies along the segments of the topographic gradient at the IBGE Reserve, Brasília-DF, Brazil. A and B – Cerrado sensu stricto; C and D – Campo Cerrado and E – Campo Sujo. GWL – groundwater level at the study site (November 2007). Data for soil samples and GWL retrieved from Rossatto et al. (2012).

In contrast, superficial water tables limit the presence of woody savanna species which are normally intolerant to waterlogging (Joly and Crawford, 1982). The success of herbaceous plants under such conditions requires adaptations to deal with frequent waterlogging, which allow them to outcompete woody species and be more diverse and richer in such conditions (Munhoz et al., 2008). In cases where herbaceous species outcompete woody species under upland conditions other important abiotic factors might be the key to explain vegetation gradients. Synergies between disturbance regimes, nutrient availability and species composition, can lead to resilient low-diversity systems in the study region, where tradeoffs between nutrient and water requirements and adaptations to fire reinforce woodlands and grasslands as alternate stable states (Silva et al., 2013). These factors have typically been considered separately from water niche differentiation (Scholz et al., 2008; Hoffmann et al., 2009; Bustamante et al., 2012), but here we propose that multiple overlapping processes involving disturbance, nutrient and water use strategies need to be considered together to understand past and predict future variations in vegetation composition and structure.

Only a few woody species in our study appeared to extract water from the deeper layers of the soil profile (>2 m, see woody species signatures in Fig. 1) It should be pointed out that we have sampled a limited number of woody species of a relative small size and restricted our sampling to the wet season. In addition to differences in patterns of water uptake among cerrado woody species, there is strong evidence to support that several cerrado woody species that form denser and taller vegetation physiognomies, rely on water from deeper soil layers and that water uptake shifts to greater depths during the dry season (Goldstein et al., 2008; Ferreira et al., 2007). However these differences would only reinforce our findings that woody and herbaceous cerrado plants partition soil water reserves. At the community level, this implies that denser cerrado woody communities are extracting water from the whole soil profile down to the water table, while more open vegetation types extract water predominantly from shallower soil depths. Furthermore, our findings are also in accordance with previous studies in Neotropical savanna which showed that groundwater depth and tolerance to intermittent flooding are important factors controlling vegetation structure and composition (Oliveira-Filho et al., 1989; Scholz et al., 2008; Child et al., 2010).



**Fig. 3.** The effect of growth form (A) and topographic gradient position (B) in the  $\delta^{18}\text{O}$  signatures of plant stem water according factorial ANOVA. Different lowercase letters indicate differences between growth forms and gradient position according to Tukey's test ( $P < 0.05$ ). In (B): A and B – Cerrado sensu stricto; C and D – Campo Cerrado and E – Campo Sujo. Vertical bars indicate standard error of means.

## Acknowledgments

Authors would like to acknowledge the Brazilian National Council of Research (CNPq) for financial support (grants n474510/2008-5, 141624/2009-4).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2013.11.011>.

## References

- Araya, Y.N., Silvertown, J., Gowing, D.J., McConway, K.J., Linder, H.P., Midley, G., 2010. A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist* 189, 253–258.
- Bustamante, M.M., Brito, D.Q., Kozovits, A.R., Luedemann, G., Melo, T.R.B., Pinto, A.R., 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 Ecology* 213, 795–808.
- Child, M.F., Milton, S.J., Dean, R.W.J., Lipsey, M.K., Puttick, J., Hempson, T.N., Mann, G.K., Babiker, H., Chaudrey, J., Humphrey, G., Joseph, G., Okes, N.C., Potts, R., Wistebaar, T., 2010. Tree-grass coexistence in a flood-disturbed, semi-arid savanna system. *Landscape Ecology* 25, 315–326.
- Dawson, T.E., Mambelli, S., Plamboeck, A., Templer, P., Tu, K., 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33, 507–559.
- Désilets, P., Houle, G., 2005. Effects of resource availability and heterogeneity on the slope of the species-area curve along a floodplain-upland gradient. *Journal of Vegetation Science* 16, 487–496.
- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. *Oecologia* 117, 504–512.
- Eiten, G., 1972. The cerrado vegetation of Brazil. *Botanical Review* 38, 201–349.
- Eggemeyer, K.D., Awada, T., Harvey, F.E., Wedin, D.A., Zhou, X., Zanner, C.W., 2008. Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C4 grasses in a semiarid grassland. *Tree Physiology* 29, 157–169.
- Ferreira, J.N., Bustamante, M., Garcia-Montiel, D.C., Caylor, K.K., Davidson, E.A., 2007. Spatial variation in vegetation structure coupled to plant available water determined by two-dimensional soil resistivity profiling in a Brazilian savanna. *Oecologia* 153, 417–430.
- Furley, P.A., 1996. The influence of slope on the nature and distribution of soils and plant communities in the central Brazilian cerrado. In: Anderson, M.G., Brooks, S. (Eds.), *Advances in Hillslope Processes*. Wiley, London, pp. 327–346.
- Furley, P., 1999. The nature and diversity of Neotropical savanna vegetation with particular reference to the Brazilian cerrados. *Global Ecology and Biogeography* 8, 223–241.
- Goldstein, G., Meinzer, F.C., Bucci, S.J., Scholz, F.G., Franco, A.C., Hoffmann, W.A., 2008. Water economy of Neotropical savanna trees: six paradigms revisited. *Tree Physiology* 28, 395–404.
- Gottsberger, G., Silberbauer-Gottsberger, I., 2006. Life in the Cerrado: a South America Tropical Seasonal Ecosystem. V. I Origin, Structure, Dynamics and plant use. Reta Verlag, Ulm.
- Grime, J.P., 2001. *Plant Strategies, Vegetation Process, and Ecosystem Properties*, 2nd ed. Wiley & Sons.
- Higgins, S.I., Delgado-Cartay, M.D., February, F.C., Combrink, I.I.J., 2011. Is there a temporal niche separation in the leaf phenology of savanna trees and grasses? *Journal of Biogeography* 38, 2165–2175.
- Hoffmann, W.A., Adasme, R., Haridasan, M., Carvalho, M.T., Geiger, E., Pereira, M.A.B., Gotsch, S.B., 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.
- Hold, R.M., 2013. Revisiting the two-layer hypothesis: coexistence of alternative functional rooting strategies in savannas. *PLoS One* 8, e69625.
- Jackson, P.C., Meinzer, F.C., Bustamante, M.M.C., Goldstein, G., Franco, A.C., Rundel, P.W., Caldas, L.S., Iglar, E., Causin, F., 1999. Partitioning of soil water among tree species in a Brazilian cerrado ecosystem. *Tree Physiology* 19, 717–724.
- Joly, C.A., Crawford, R.M.M., 1982. Variation in tolerance and metabolic responses to flooding in some tropical trees. *Journal of Experimental Botany* 33, 799–809.
- Medina, E., Silva, J.F., 1990. Savannas of northern South America: a steady-state regulated by water–fire interactions on a background of low nutrient availability. *Journal of Biogeography* 17, 403–413.
- Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavellier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121, 293–301.
- Mckane, R.B., Johnson, L.C., Shaver, G.R., Nadelhofer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G., 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415, 68–71.
- Munhoz, C.B.R., Felfili, J.M., Rodrigues, C., 2008. Species-environment relationship in the herb-subshrub layer of a moist Savanna site, Federal District, Brazil. *Brazilian Journal of Biology* 68, 25–35.
- Nippert, J.B., Knapp, A.K., 2007. Soil water partitioning contributes to species existences in tallgrass prairie. *Oikos* 116, 1017–1029.
- 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. *Functional Ecology* 19, 574–581.
- Oliveira-Filho, A.T., Shepherd, G.J., Martins, F.R., Stubblebine, W.H., 1989. Environmental factors affecting physiognomic and floristic variation in an area of Cerrado in central Brazil. *Journal of Tropical Ecology* 5, 413–431.
- Oliveira-Filho, A.T., Ratter, J.A., 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil*. Columbia University Press, New York, pp. 121–140.
- Querejeta, J.I., Estrada-Medina, H., Allen, M.F., Jimenez-Osornio, J.J., 2007. Water source partitioning among trees growing on shallow karst soil in a seasonally dry tropical climate. *Oecologia* 152, 26–36.
- Rossatto, D.R., Silva, L.C.R., Villalobos-Vega, R., Sternberg, L.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. *Environmental and Experimental Botany* 77, 259–266.
- Rossatto, D.R., Sternberg, L.S.L., Franco, A.C., 2013. The partitioning of water uptake between growth forms in a Neotropical savanna: do herbs exploit a third water source niche? *Plant Biology* 15, 84–92.
- Saha, A.K., Sternberg, L.S.L., Miralles-Wilhelm, F., 2009. Linking water sources with foliar nutrient status in upland plant communities in the Everglades National Park, USA. *Ecohydrology* 2, 42–54.
- Sales, N.M., Pérez-García, F., Silveira, F.A.O., 2013. Consistent variation in seed germination across an environmental gradient in a Neotropical savanna. *South African Journal of Botany* 87, 129–133.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S., Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. *Nature* 438, 846–849.
- Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral roots spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90, 480–494.
- Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Salazar, A., 2008. Plant- and stand-level variation in biophysical and physiological traits along a tree density gradient in the Cerrado. *Brazilian Journal of Plant Physiology* 20, 217–232.
- Silberbauer-Gottsberger, I., Eiten, G., 1987. A hectare of cerrado. I. General aspects of the trees and thick-stemmed shrubs. *Phyton* 27, 55–91.
- Silva, L.C.R., Hoffmann, W.A., Rossatto, D.R., Haridasan, M., Franco, A.C., Howarth, W., 2013. Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. *Plant and Soil*. <http://dx.doi.org/10.1007/s11004-013-1822-x> (Online-Early).
- Staver, A.C., Archibald, S.A., Levin, S.A., 2011. Tree cover in sub-Saharan Africa: rain-fall and fire constrain forest and savanna as alternative stable states. *Ecology* 92, 1063–1072.
- Vendramini, P.F., Sternberg, L.S.L., 2007. A faster plant stem-water extraction method. *Rapid Communications in Mass Spectrometry* 21, 164–168.
- Verweij, R.J.T., Higgins, S.I., Bond, W.J., February, E.C., 2011. Water sourcing by trees in a mesic savanna: responses to severing deep and shallow roots. *Environmental and Experimental Botany* 74, 229–236.
- Villalobos-Vega, R., 2010. Water table and nutrient dynamics in neotropical savannas and wetland ecosystems. (Ph.D.) University of Miami, Miami, Florida.
- Walter, H., 1971. *Natural Savannas. Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, UK.
- Ward, D., Wiegand, K., Getzin, S., 2003. Walter's two-layer hypothesis revisited: back to the roots! *Oecologia* 172, 617–630.
- Yang, H., Auerwald, K., Bai, Y., Han, X., 2011. Complementarity in water sources among dominant species in typical steppe ecosystems of Inner Mongolia, China. *Plant and Soil* 340, 303–313.