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Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna

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ABSTRACT

Vegetation structure of the savannas is variable across the landscape, ranging from open grassland to savanna woodland within topographic gradients of a few hundred meters in length. Here we investigated whether patterns of soil water extraction by the woody layer and vegetation structure changed in response to groundwater depth. We determined depth of plant water uptake, groundwater level and vegetation structure on five different locations along a topographic gradient in the highlands of Central Brazil. The elevation gradient of about 110 m covered all vegetation physiognomies generally associated with topographic gradients in savannas of Central Brazil. To estimate the depth of plant water uptake in the different slope positions we relied on comparisons of hydrogen and oxygen isotope ratios of plant stem water, water from different soil depths, from groundwater and from rainfall. We subsequently used a stable isotope mixing model to estimate vertical partitioning of soil water by woody plants along the elevation gradient. We were able to show that groundwater level affected plant water uptake patterns and soil water partitioning among savanna woody species. Vegetation at higher elevation extracted water from deeper unsaturated soils and had greater variability in water uptake strategies, which was coupled to a denser and more complex woody layer. Plants on these soils used stored water from both shallow (<0.6 m) and deep (0.6–2.00 m) soil layers. At lower elevation sites, however, the presence of a water table near the soil surface restricted water uptake to the shallower wet season unsaturated zone of the soil profile. The sparser woody vegetation is probably composed of species that only rely in superficial water uptake, or are plastic in relation to root characteristics.

1. Introduction

Tropical savannas consist of dynamic mixtures of trees and grasses that result in a mosaic of different physiognomic forms across the landscape. As such, tropical savannas are characterized by great variation in resource availability at global, regional and local scales (Bourliere, 1983; Sarmiento, 1983; Gottsberger and Silberbauer-Gottsberger, 2006). Soil properties and especially soil water regimes play an important role on regulating the composition of species and their functional aspects (Bourliere, 1983; Franco, 2002; Sankaran et al., 2005; Haridasan, 2008). A special case of vegetation variation occurs on topographic gradients in savannas of Africa, Australia and South America (Furley et al., 1992; Ratter et al., 1997). In these savannas vegetation structure and species composition vary heavily across the landscape, ranging from open grassland to savanna woodland and forest sometimes within distances of a few hundred meters (Furley, 1996; Oliveira-Filho and Ratter, 2002).

Variations in vegetation structure are frequently related to changes in topography in savannas of Central Brazil, locally known as "cerrado", the second most extensive plant formation in South America (Eiten, 1972; Furley, 1996). In the upper portion of the topographic gradient over deep oxisols, woody savannas (locally called cerrado *sensu stricto*) are usually the dominant vegetation (Silberbauer-Gottsberger and Eiten, 1987). Tree density decreases and soils become shallower towards lower elevations while the groundwater approaches the surface. Open shrubby savanna formations (*campo cerrado*) and vegetation with a few very low trees (open shrubby grasslands, regionally called *campo sujo*) become more common and eventually wet grasslands can be found at lower elevations on seasonally waterlogged soils (Eiten, 1972; Silberbauer-Gottsberger and Eiten, 1987; Furley, 1999).

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Structural variations along these topographic gradients are assumed to be the result of changes in soil physical and chemical traits (Eiten, 1972; Oliveira-Filho and Ratter, 2002), or fire frequency (Durigan and Ratter, 2006). For example, the presence of concretions, soil texture, aluminum concentration, nitrogen mineralization potential and available phosphorus, which often vary along topographical gradients, are thought to define not only the functional aspects of individual species but the spatial distribution of woody plant communities as well (Goodland and Pollard, 1973; Ruggiero et al., 2002; Sankaran et al., 2008). Indeed there are studies suggesting that such edaphic traits act as filters on the selection of plants with particular resource use strategies (Goodland, 1971; Haridasan, 2008), but results have been mostly inconclusive. Soil water regimes on the other hand are thought to play primary roles in the distribution of species and vegetation physiognomies within small watersheds, especially the minimum distance between the soil surface to the water table (Haridasan, 2008; Villalobos-Vega, 2010). The majority of woody savanna plants are not tolerant to high soil-moisture levels, which is a common situation on downslope regions of topographic gradients, where the groundwater can be very close or cover the soil surface during the wet season (Eiten, 1972; Oliveira-Filho et al., 1989; Furley, 1999; Ruggiero et al., 2006; Gottsberger & Silberbauer-Gottsberger, 2006; Child et al., 2010). The anoxic conditions of downslope soils impair root growth of savanna plants and lead to plant death (Joly and Crawford, 1982).

Little attention has been dedicated to water use along topographical gradients and its associated changes on vegetation structure (Schenk and Jackson, 2002; Goldstein et al., 2008). The amount and quality of available water has been considered of high relevance in explaining functional plant diversity in diverse ecosystems around the world (Romero-Saltos et al., 2005; Ewe et al., 2007; Greaver and Sternberg, 2010). Variations in elevation over short distances and associated changes in soil water resources could clearly affect plant traits related to plant water balance and water use. Studies have shown differences in sap flow fluxes, woody density, water potential, leaf size and specific leaf area of woody species growing in different positions along topographic gradients (Barij et al., 2007; Scholz et al., 2008b; Dulamsuren et al., 2009; Kooyman et al., 2010). These modifications on hydraulic properties and on plant water loss are evidence that partitioning of soil water resources by the woody vegetation could change along topographical gradients. However, these studies have focused primarily on aboveground features of the woody vegetation. They did not determine whether these changes on structure and hydraulic characteristics of the woody vegetation would also result in adjustments in the use of belowground resources, particularly on patterns of soil water extraction by the vegetation.

In this study we tested two hypotheses: First, since woody savanna species are intolerant of high soil moisture and flooding (Joly and Crawford, 1982), we hypothesized that at lower elevations of the topographic gradient, where the wet season groundwater level is high, plant water uptake is restricted to the surface layers of the soil profile. Second, we asked whether an increase in the contribution of plant water extraction from deeper unsaturated soils at higher elevation is related to an increase in the complexity of woody vegetation. To estimate the depth of plant water uptake we relied on comparisons of hydrogen and oxygen isotope ratios of plant stem water, soil pore water collected at different depths and from groundwater (Dawson et al., 2002). These data were used as input to a stable isotope mixing model (Phillips and Gregg, 2003) to estimate vertical partitioning of soil water extraction by woody plants along the topographical gradient.

2. Methods

2.1. Study area and species selection

The study was conduced at the IBGE Ecological Reserve, located 33 km south of Brasília in Brazil (15°56′S, 47°53′W) with an average altitude of 1100 m. The average annual precipitation is approximately 1500 mm with a pronounced dry season from May through September. Mean monthly temperature ranges from 19 to 23 °C. The predominant soils at the study site are deep well drained Oxisols, but Cambisols and Hydromorphic soils also occur associated with hill slopes and valley bottoms respectively.

We employed a transect of 1500 m spanning an elevation gradient of about 110 m, covering all vegetation physiognomies generally associated with topographic gradients in the cerrado region. We subdivided the transect in 5 segments following the changes in vegetation physiognomies from the highest to the lowest elevation. The two first segments of the transect (A and B) supported typical savanna vegetation, locally known as cerrado *sensu stricto*. Segments C and D were covered by a more open shrubby savanna, known as *campo cerrado*, while segment E was covered by a very open (near treeless) physiognomy, known as *campo sujo*. In each of these segments we measured tree diameter and height, tree density and basal area. This was done in four 4 × 4 m (16 m^2) plots per segment. We surveyed all woody species with a minimum stem diameter of 2 cm at 30 cm above ground level, but only 10–14 mature individuals (>6 cm in diameter) were sampled at each topographical location (Table 1).

2.2. Defining water source of the most common woody species

The oxygen and hydrogen isotopic composition (δ^2H and δ^{18}O) of the stem, soil, groundwater and rainfall were determined. Stem samples of a large range of species (Table 1), one individual per species in each location, were collected at each of the five locations. This did not allow comparisons among species but rather allowed to distinguish differences between woody plant communities at different topographic positions (Hurlbert, 1984). 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

Table 1
Species and their occurrence at the segments along the topographic gradient. A and B: cerrado *sensu stricto*, C and D: *campo cerrado* and E: *campo sujo*.

Species	Vegetation type
Anacardium humile A.St.-Hil.	A, B, C
Allagoptera campestris (Mart.) Kuntze	E
Bauhinia pulchella Benth.	D, E
Byrsonima crassa Nied.	A, B, D, E
Calliandra dysantha Benth.	D
Dalbergia miscolobium Benth.	A, C, E
Guapira noxia (Netto) Lund.	A, D
Hymenaea stigonocarpa Mart. ex Hayne	A, B
Kielmeyera coriacea Mart.	D, E
Miconia ferruginata DC.	A, D
Ouratea hexasperma (A.St. Hil.) Baill.	A, B, C
Palicourea rigida Kunth	A, B
Qualea grandiflora Mart.	E
Roupala montana Aubl.	D, E
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	C, E
Sclerolobium paniculatum Vog.	A, B
Stryphnodendron adstringens (Mart.) Coville	A, B, C, D, E
Styrax ferrugineus Nees. & Mart.	D
Syagrus comosa (Mart.) Becc.	A, B, C, D
Syagrus flexuosa (Mart.) Becc.	A, D, E
Symplocos rhamnifolia A.D.C.	A, B, C, D

container. Samples were collected from adult individuals in a sunny day in 18th November 2007 during the wet season, after a period of two weeks without rainfall. Collection of data was made only in wet season as the minimum distance between soil surface and water table depth (achieved on wet season) appears to be the major environmental factor that accounted for changes in tree density and in tree radial growth along the topographic gradient (Villalobos-Vega, 2010). Soil samples were also collected at each of the five sampling areas to determine variations in δ^2H and δ^{18}O across different depths of the soil profile. Soils were collected in intervals of 20 cm down to 2 m depth or until the groundwater was reached. Variations in the groundwater level at the five study sites along the topographic gradient were monitored by automated submersible pressure sensors (Solinst – Levelogger, Model 3001 F30/M10) installed in wells (depth of about 1–12 m, depending on the level of the water table). Groundwater samples were also collected from those wells. Rainfall was collected monthly between October 2007 (previous to this study) and November 2009 with rain collectors installed in open sites near the study site at the IBGE reserve. The collectors consisted of a funnel attached to a bottle having a mineral oil layer approximately 1 cm thick to prevent evaporation.

The water extraction from plant stems and soils was conduced at the Plant Physiology Laboratory of the University of Brasília, and followed the methodology described by Vendramini and Sternberg (2007). Water obtained from the wells (groundwater) and 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 δ^{18}O and δ^2H values respectively and calculated as:

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

where R_{sample} and R_{SMOW} represents 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 (Saha et al., 2009).

We calculated the average frequency of water uptake for each studied location, using δ^2H and δ^{18}O stem signatures of each collected species. For this we used the software IsoSource Version 1.3 (Phillips and Gregg, 2003). The obtained values were averaged and the mean frequency taken as the frequency of water uptake by the vegetation at each selected location along the transect. To make a distinction between shallow and deep soils we considered shallow soils to be the region in the soil profile above 60 cm (Dawson et al., 2002). We assumed here that the bulk of plant water uptake during the wet season occurred within the range of depth where soil water was collected and analyzed for hydrogen and oxygen isotope ratios (0–2 m).

2.3. Statistical analysis

Differences in plant stem isotope water signature (δ^2H and δ^{18}O), frequency of water uptake on shallow soils and phytosociological parameters were verified through an ANOVA followed by Tukey's test ($\alpha = 0.05$). All data presented normality ($P > 0.45$ according to the Kolmogorov–Smirnov test) and homogeneity of variances, according to the Levene's test ($F_{1,65} = 1.24$, $P = 0.29$). Linear regression was used to test for relationships between groundwater depth during the wet season (measured on the same day of plant sampling for isotope analysis) and the frequency of water uptake on shallow soils. A linear regression was performed to test if the fraction of water uptake on deep soils was related to plant height, basal area and other phytosociological parameters of the vegetation. All the analysis were made using STATISTICA 7.0 package. Differences between stem water, rainfall and soils in the δ^{18}O and δ^2H relationship were tested with the SMATR software (Warton et al., 2006).

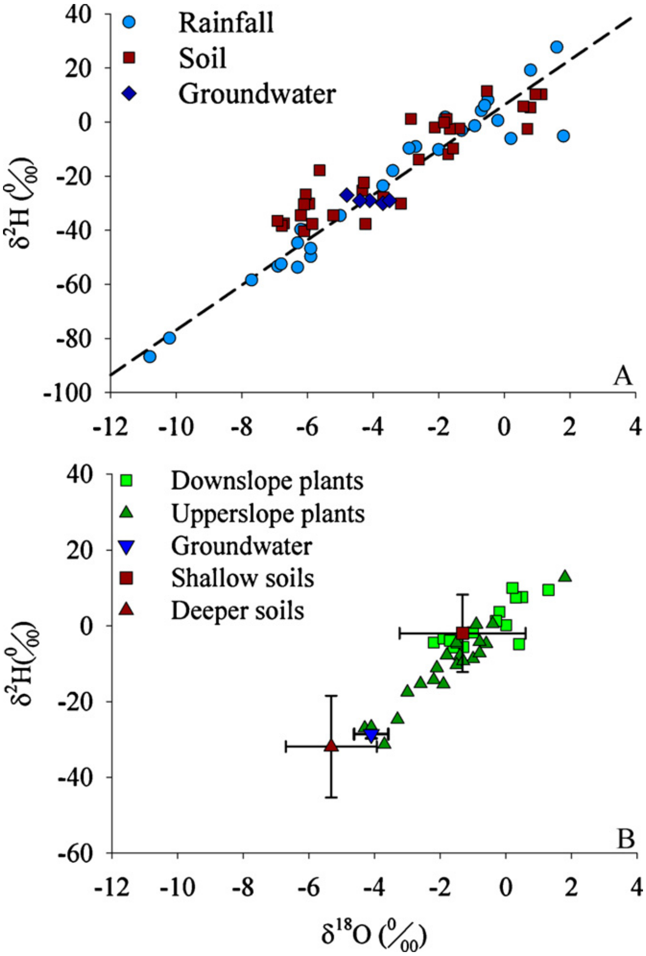

Fig. 1. The δ^2H and δ^{18}O signatures of rainfall, soils and groundwater (A) and δ^2H and δ^{18}O signatures of plant stem water and averages of the potential sources of water collected at different positions along the topographic gradient (B). Regression line for rainfall water: $\delta^2\mathrm{H} = 8.3\delta^{18}\mathrm{O} + 6.33$, $r^2 = 0.993$, $P < 0.01$. Upperslope plants represent the isotope signatures of plants at locations A, B and C; downslope plants represent the isotope signatures of plants at locations D and E.

3. Results

3.1. Rainfall, soil and groundwater isotopic composition

A plot of the δ^2H versus the δ^{18}O values of rainfall water (Fig. 1A) fell in a line with a slope of 8.3 and an intercept of 6.33, and not significantly different from the global meteoric water line (GMWL, $\delta^2\mathrm{H} = 8\delta^{18}\mathrm{O} + 10$, Wald Statistic = 0.03, $P = 0.95$). The δ^2H and δ^{18}O values of wet season soil water also fell very near the global meteoric water line, showing no significant difference to the slope of the GMWL ($Y = 6.107x + 3.48$, $r^2 = 0.88$, $P < 0.05$, Wald Statistic = 0.70, $P = 0.67$).

Although isotope ratios fell in a line with a similar slope as the GMWL during the wet season, there was a significant variation within soil profiles in the δ^2H and δ^{18}O signatures for the different locations along the transect (Fig. 2). In all cases, water from

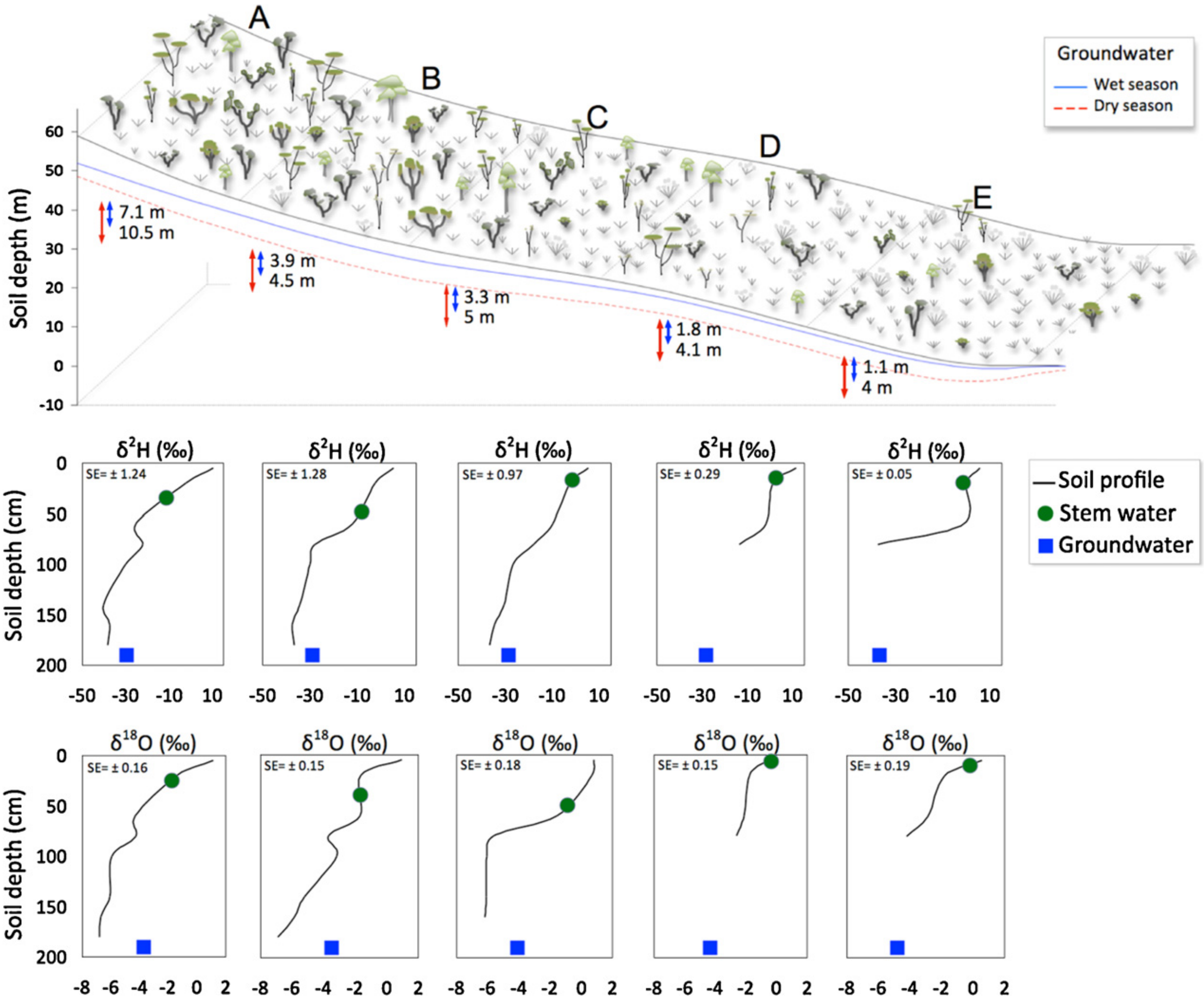

Fig. 2. Soil water (black lines), groundwater (blue square) and averages of the woody community plant stem water (green circle) signatures for δ^2H and δ^{18}O of different physiognomies along the segments of the topographic gradient at the IBGE reserve, Brasília-DF, Brazil. A and B – cerrado *sensu stricto*; C and D – *campo cerrado* and E – *campo sujo*. Maximum (during dry season, red dotted line) and minimum (during wet season, blue solid line) values of groundwater depth are also depicted. SE indicates standard error of means for stem water at each segment of the transect (n = 11–14 species). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

the superficial layers of the soil profile was isotopically enriched compared to the deeper layers, whose soil water δ^2H and δ^{18}O values tended to be similar to the groundwater signature (Fig. 2). Soils from upper slope elevations had the most pronounced variations in isotopic composition, while oxygen and hydrogen isotopic composition along the soil profile at lower sampling sites (locations D and E in Fig. 2), rapidly approached values measured for the groundwater (Fig. 2).

The δ^{18}O values of groundwater at the lower positions on the transect were little more depleted (between −4.4 and 4.8‰) compared with those at higher elevations along the transect (−3.5 and −3.7‰), however this 1‰ difference may not be ecologically significant, as in soil water, the δ^{18}O and δ^2H of the groundwater samples also fell close to the GMWL (Fig. 1A). Groundwater depth along the topographic gradient varied between 7.00 ± 0.03 m (higher elevations) and 1.00 ± 0.11 m (lower elevations) (Fig. 2). Groundwater depth pronouncedly increased during the dry season, being as much as 3.00 ± 0.93 m deeper at each sampling location (Fig. 2).

3.2. Isotopic composition of stem water

As in rainwater, soil water and groundwater, δ^2H and δ^{18}O values of plant stems also fell close to the meteoric water line ($Y = 7.130 + 1.24$, $r^2 = 0.91$, $P < 0.05$, Wald Statistic = 0.04, $P = 0.89$). However, there were significant differences in stem water isotopic composition among the woody species assemblages from different locations along the slope (Figs. 1B and 2) both in terms of δ^2H (ANOVA, $F_{5,65} = 9.16$, $P = 0.002$) and δ^{18}O (ANOVA, $F_{5,65} = 4.82$, $P = 0.001$). The range of stem water δ^2H and δ^{18}O values was greater for plants growing at higher elevation sites compared to those at lower elevation sites along the transect (Fig. 1B).

Woody plants at higher elevations along the transect (segments A and B) had more negative (Tukey's test < 0.05) δ^2H and δ^{18}O values of stem water compared to those at lower elevations (segments C, D and E) along the transect (Figs. 1 and 2). Plants at lower elevations had stem water isotopic signatures indicating that they were mostly relying on superficial soils (0.10–0.60 m) for water uptake. This was corroborated by the frequency of water uptake from shallow soils estimated for the five different locations along the topographical gradient (Fig. 3). The woody community at higher elevation sites (sites A, B and C) acquired approximately 70–80% of their stem water from pore water from superficial soil layers. This was significantly less ($F_{5,65} = 9.90$, $P < 0.001$) than that utilized by plants at lower elevation sites (sites D and E), which used almost exclusively water from the superficial soil layers (90–100%). The clear relationship between groundwater depth in wet season

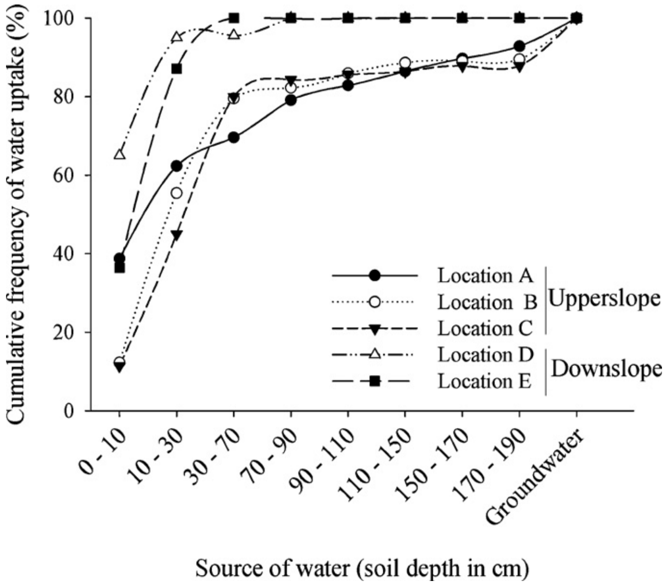

Fig. 3. Cumulative frequency of water uptake on different locations along the studied transect with the following vegetation: A and B – cerrado *sensu stricto*; C and D – *campo cerrado* and E – *campo sujo*.

and frequency of water uptake from shallow soils (Fig. 4, $r^2 = 0.90$, $P = 0.013$) is a strong indication that groundwater depth plays an important role in defining the water uptake by woody plants during the wet season.

3.3. Water uptake patterns and vegetation structure along the topographic gradient

There were significant changes in woody vegetation properties along the studied transect (Fig. 5). Basal area ($F_{4,15} = 29.48$, $P < 0.001$), stem density ($F_{4,15} = 6.59$, $P < 0.001$), average plant height ($F_{4,15} = 16.36$, $P < 0.001$) and average tree diameter ($F_{4,15} = 14.98$, $P < 0.001$) differed along the topographic gradient (Fig. 5). Only few species occurred in all sites (Table 1) but the structural changes in the vegetation allowed a clear distinction of the phytophysiognomies associated with the topographic change. Sites at higher elevation had higher total basal area (Fig. 5A), plant density (Fig. 5B), height (Fig. 5C) and diameter (Fig. 5D) then those at lower elevations.

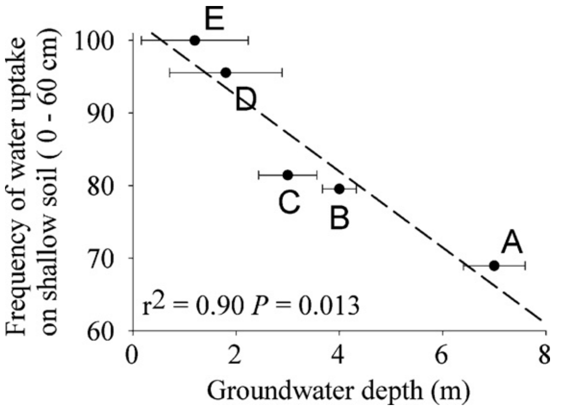

Fig. 4. Relationship between groundwater depth and the frequency of water uptake from shallow soils used by each plant community along the topographic gradient. Letters indicate segments of the transect with the following vegetation: A and B – cerrado *sensu stricto*; C and D – *campo cerrado* and E – *campo sujo*. Horizontal bars indicate standard error of the mean.

There was a clear and positive relationship (Fig. 6) between frequency of water uptake on deep soil and the vegetation properties of each segment ($r^2 > 0.84$ and $P < 0.05$). In this manner, an increase in the contribution of plant water extraction from deeper unsaturated soils at higher elevation is related to an increase in the complexity of woody vegetation.

4. Discussion

4.1. Soil patterns

Our results differ from several studies (Ewe et al., 2007; Querejeta et al., 2007; Saha et al., 2009) that reported an oxygen isotopic enrichment of water from surface layer of the soil profile due to evaporation. The relationship between δ^2H and δ^{18}O obtained from water extracted at different depths of the soil profiles fell within the meteoric rainfall line (Fig. 1A). This provides evidence that the rainfall events during the wet season are frequent enough to damp the expected evaporative isotopic enrichment of the superficial soil layers. On the other hand, even though δ^2H and δ^{18}O values of soil water fell close to the GMWL, the observed isotopic enrichment of soil water from the surface layers at all sites suggests evaporation under isotopic equilibrium with little kinetic effects (Clark and Fritz, 1997).

4.2. Plant water uptake patterns changes along the topographic gradient

Plants from higher slope positions of the transect, with a relatively deep water table (~7 m depth) extracted significantly more water from deeper soil layers (>0.60 cm) than plants growing at lower slope positions, where water uptake tends to be restricted to the superficial soil layers (Fig. 3), as groundwater is very near the soil surface. The greater depth 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).

We estimated that at least 30% of the water acquired by the woody community at the higher elevation sites of the transect originated from deeper layers of the soil profile (including groundwater) with the remaining water coming from superficial soil layers. These results are consistent with the presence of dimorphic root systems in many cerrado woody species, which enable them to extract water from superficial and deeper soil layers (Scholz et al., 2008a). Despite possible variation in root depth among individual species, our results are also consistent with reports that cerrado woody species at the community level have most of the fine roots in the first 0.5-m of the soil profile (Oliveira et al., 2005).

Woody species, therefore, appear to rely mostly on soil water from shallow soil layers for water balance, at least during the wet season, when rains are very frequent (Dodd et al., 1998; Verweij et al., 2011). Groundwater resources could be more important during the dry season, as in some Australian savannas where at least 50% of water used for transpiration in some species come from these deeper water resources during the dry season (Lamontagne et al., 2005). In fact, there are evidences that several cerrado woody species, at least in typical denser vegetation sites, rely on water sources from deeper regions of the soil profile (around 1.5–3 m) during the dry season (Goldstein et al., 2008), which suggests that there is a niche separation between woody plants and grasses in which the latter only use water from the upper soil layers, whereas trees can use water from both upper and deeper layers. This plasticity in water uptake patterns has been considered an important strategy to allow the co-existence of a diversified plant community in water-limited systems (Eggemeyer et al., 2008; Yang et al., 2011).

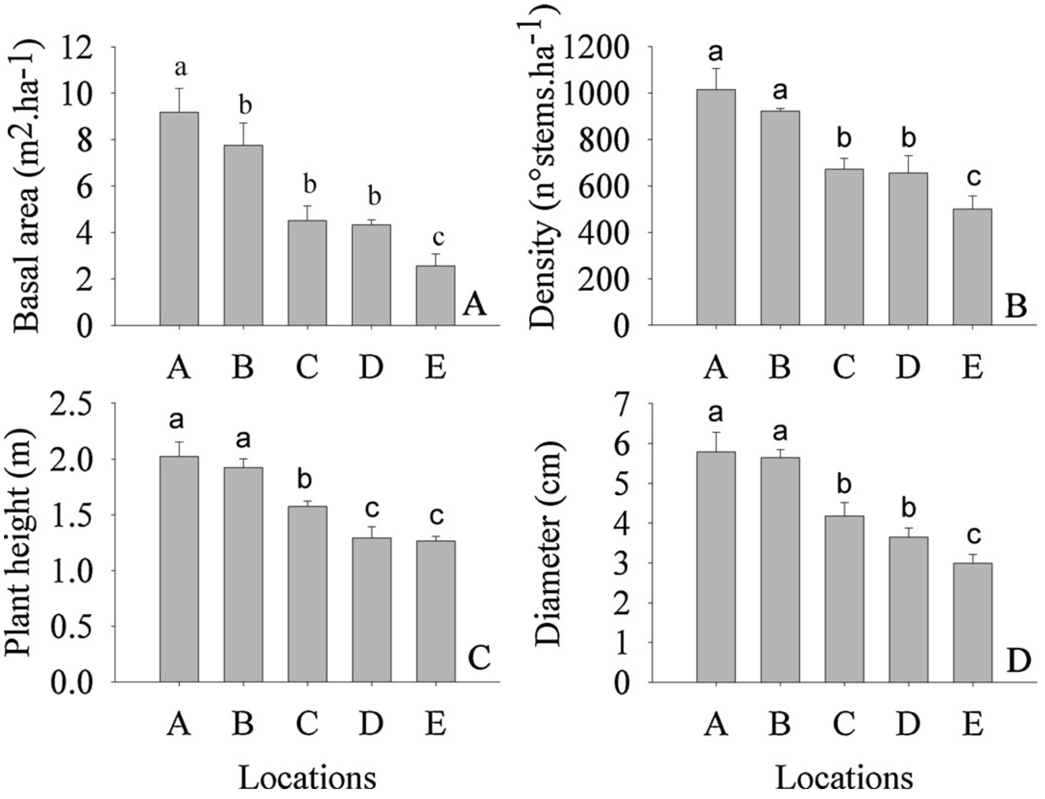

Fig. 5. Structural parameters of the woody vegetation at the five different locations along the topographic gradient. A: basal area; B: tree density; C: plant height and D: diameter. Values with different smallcase letters demonstrates differences according Tukey's test ($P < 0.05$). Vertical bars indicate standard error of means. Locations: A and B: cerrado *sensu stricto*; C and D: *campo cerrado* and E: *campo sujo*.

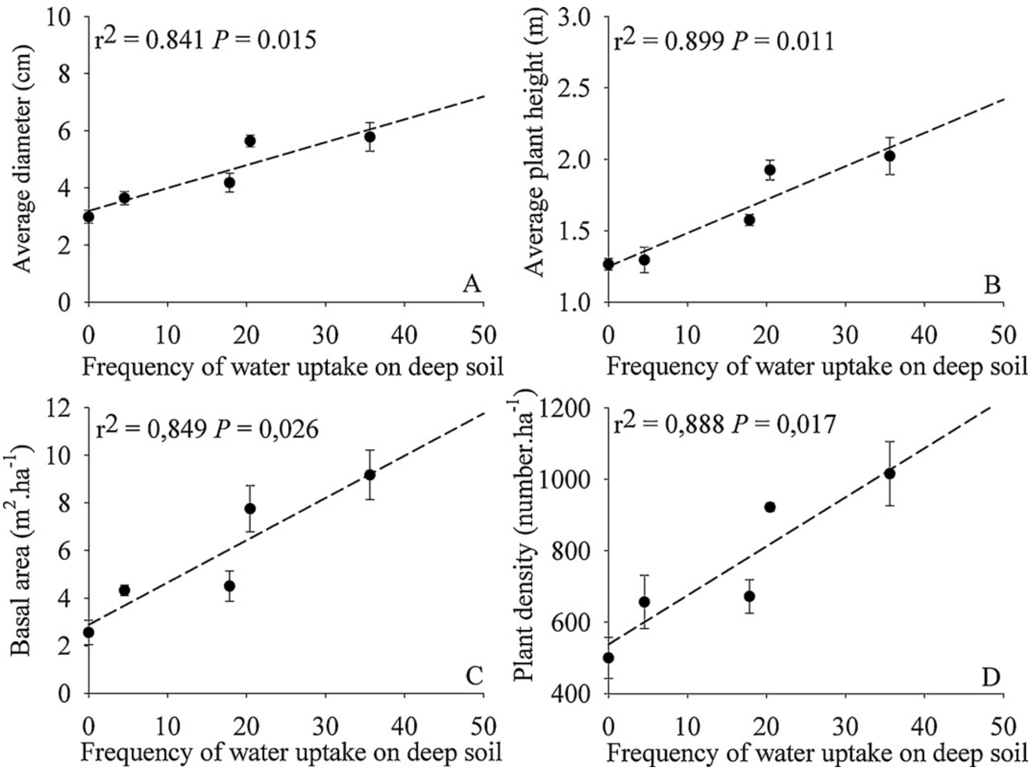

Fig. 6. Relationships between frequency of water uptake from deep soil and vegetation parameters: A: average plant diameter (cm); B: average plant height; C: basal area ($m^2\ ha^{-1}$) and D: plant density (no. ha^{-1}). Linear regression was applied. R^2 and P values were shown. Vertical bars indicate standard error of the mean ($n = 4$).

The results presented here suggest that woody plants at higher locations have a greater range in depth of soil water extraction allowing different species to coexist, which is in line with the frequently discussed "Walter's two-layer hypothesis" (Walter, 1971). This hypothesis suggests that there is a niche separation between woody plants and grasses in which the latter only use water from the upper soil layers, whereas trees can use water from both upper and deeper layers of the soil profile (Walter, 1971; Schenk and Jackson, 2002). Cerrado woody species display a variety of root systems from shallow-rooted, dimorphic to deep-rooted (Rawitscher, 1948; Scholz et al., 2008a). The results of this community level study confirm this broad range of water extraction patterns in woody species, which are however, dependent on the depth of the water table.

While cerrado woody species are apparently able to successfully tap both superficial and deep water sources in unsaturated upperslope soils, the presence of a water table near the soil surface downslope affected water uptake patterns. These high levels of groundwater during the wet season can greatly constrain the establishment of woody plants (Eiten, 1972) (Fig. 2). Cerrado plants and other woody savanna plants are intolerant to waterlogging, as indicated by their low rates of biomass accumulation and also a higher number of dead plants when they have their roots exposed to flood (Joly and Crawford, 1982; Child et al., 2010). Hypoxic conditions in downslope due to high groundwater levels may be determinant in maintaining differences in water uptake along slope gradients (Désilets and Houle, 2005; Child et al., 2010). Nonetheless, some species such as *Stryphnodendron adstringens*, were found in all portions of the slope gradient, including on sites where groundwater is superficial (Table 1). The occurrence of this species in higher and lower slope positions indicates that it can successfully change its growth patterns and its water uptake in order to survive these contrasting conditions. In fact, it has been shown that some common tree species from cerrado (*e.g. Tabebuia aurea*) can survive and grow in flooded soil conditions by reducing shoot height and aboveground biomass, and having higher investment in superficial roots (Cabral et al., 2004).

4.3. The water uptake and vegetation structure

Water uptake patterns are strongly linked to vegetation structure. The clear relationship between frequency of water uptake on shallow soil and groundwater depth (Fig. 4) as well as the tight correlation between the frequency of water uptake on deep soil and all studied phytosociological parameters (Fig. 6A–D) demonstrates that in deeper soils, where the denser physiognomies predominated, a larger range of different strategies of water uptake occurred (*e.g.* use of water from different depths). This variability in water uptake patterns may be the result of a greater range in depth of soil water extraction by plants at higher elevation sites and could help to reduce inter-specific competition allowing coexistence of a larger number of different species in the same habitat (Leffler and Caldwell, 2005). At lower elevation sites, however, a more superficial groundwater associated with shallower soil profiles could strongly restrict root growth, affecting the potential range of water uptake strategies. These restrictive conditions would also tend to limit biomass accumulation, reflecting on the low values of diameter, basal area and plant height (Fig. 5).

The increase in soil volume to be explored by the roots, that results from deeper water tables, could also affect a multitude of factors, *e.g.* nutrient uptake or the anchorage of plants in the soil. In cases where depth of groundwater is not a prevailing factor to determine the vegetation structure along slope gradients, being very deep (>10–15 m), nutrient content and fire frequency may become prominent factors (Ruggiero et al., 2002; Oliveira-Filho et al., 1989). In some cases, geological distinctiveness in these topographic gradients may act as impediments for plant anchorage such as the presence of concretions (solid bedrock or laterite crusts) at different positions along the gradient, which may limit root penetration into deeper horizons (Sarmiento, 1983; Furley and Ratter, 1988; Haridasan, 2008).

In addition, fire can exert an important role on savanna vegetation structure and function by creating conditions that are favorable to a fast re-growth of savanna grasses, leading to great accumulation of grass fuel load for future fires (Hennenberg et al., 2006; Hoffmann et al., 2009), then decreasing abundance of woody plants (Moreira, 2000). This may be true especially in lower locations of the topographic gradient where grass diversity and biomass are higher (Scholz et al., 2008b). Thus, we expect that waterlogging and fire would be the most prominent factors that act in concert to maintain the observed changes in water uptake and vegetation structure along the topographic gradient, even though no natural barriers to fire passage were present.

5. Conclusions

Here we show that the ground water level affects plant water uptake patterns and soil water partitioning among woody species. Our results suggest that plants growing in areas with a deeper wet season unsaturated soil profile have greater variability in water uptake strategies, which in turn is coupled to a denser and more complex woody vegetation. Plant water uptake at lower elevations is limited by the presence of shallow groundwater and constrained to the shallower wet season unsaturated zone of the soil profile. The existence of sparser woody vegetation is related to the presence of species that only rely in superficial water uptake, or are plastic in relation to growth strategies. The findings reported here fill a gap in our understanding of the mechanisms of water use and vegetation structure within the cerrado region and allow comparisons between analogous types of savanna vegetation elsewhere.

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