Oecologia
DOI 10.1007/s00442-007-0747-6

Spatial variation in vegetation structure coupled to plant available water determined by two-dimensional soil resistivity profiling in a Brazilian savanna

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Received: 10 May 2006 / Accepted: 31 March 2007

Abstract Tropical savannas commonly exhibit large spatial heterogeneity in vegetation structure. Fine-scale patterns of soil moisture, particularly in the deeper soil layers, have not been well investigated as factors possibly influencing vegetation patterns in savannas. Here we investigate the role of soil water availability and heterogeneity related to vegetation structure in an area of the Brazilian savanna (Cerrado). Our objective was to determine whether horizontal spatial variations of soil water are coupled with patterns of vegetation structure across tens of meters. We applied a novel methodological approach to convert soil electrical resistivity measurements along three 275-m transects to volumetric water content and then to estimates of plant available water (PAW). Structural attributes of the woody vegetation, including plant position, height, basal circumference, crown dimensions, and leaf area index, were surveyed within twenty-two 100-m^2 plots along the same transects, where no obvious vegetation gradients had been apparent. Spatial heterogeneity was evaluated through measurements of spatial autocorrelation in both PAW and vegetation structure. Comparisons with null models suggest that plants were randomly distributed over the transect with the greatest mean PAW and lowest PAW heterogeneity, and clustered in the driest and most heterogeneous transect. Plant density was positively related with PAW in the top 4 m of soil. The density-dependent vegetation attributes that are related to plot biomass, such as sum of tree heights per plot, exhibited spatial variation patterns that were remarkably similar to spatial variation of PAW in the top 4 m of soil. For PAW below 4 m depth, mean vegetation attributes, such as mean height, were negatively correlated with PAW, suggesting greater water uptake from the deep soil by plants of larger stature. These results are consistent with PAW heterogeneity being an important structuring factor in the plant distribution at the scale of tens of meters in this ecosystem.

Keywords Vegetation structure · Vegetation patterns · Cerrado · Soil moisture heterogeneity

Communicated by Todd Dawson.

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Introduction

Large spatial heterogeneity characterizes vegetation structure along tropical savannas, where a mosaic with high- and low-cover patches is created by the varied proportion of woody plants interspersed in a grass matrix (Sarmiento 1984). Most studies examining vegetation spatial patterns in savannas were conducted in arid or semi-arid areas where positive feedback between plant density and local water infiltration, coupled with the spatial redistribution of runoff water, greatly contribute to the formation of such patterns (Hillerislambers et al. 2001; Bromley et al. 1997).

Resource heterogeneity (water and nutrients) and disturbances (fire and herbivory) are the main factors assumed to control savanna structure (Frost et al. 1986). In the last decade, many studies have exposed broad spatial gradients of vegetation structure in savannas associated with patterns of increased water availability, inferred by precipitation gradients (Sankaran et al. 2005; Caylor et al. 2004, Caylor and Shugart 2004; Privette et al. 2004; Scholes et al. 2004, 2002; Williams et al. 1996). A continental-scale analysis across arid and semi-arid African savannas indicated that water availability is the factor that constrains the maximum woody cover in the savannas with mean annual precipitation (MAP) less than 650 mm, while herbivory and fire strongly mitigate measured tree distribution and abundance where MAP exceeds 650 mm (Sankaran et al. 2005). While these studies have clearly demonstrated broad spatial gradients of vegetation structure associated with patterns of increased water availability, the fine-scale heterogeneity characterizing plant community structures in association with the local distribution of soil water resources has been less well explored.

The Brazilian savannas, locally known as ‘‘Cerrado’’, are characterized by a variety of physiognomic types ranging from open treeless grasslands to almost closed-canopy woodlands (Oliveira-Filho and Ratter 2002), and are distributed along the landscape in mosaics or determining gradients. The variety of structural physiognomies differ in their above-ground biomass through their differences in structural features such as plant density, basal area, canopy cover and canopy height (Eiten 1972; Ribeiro and Tabarelli 2002). Previous studies conducted in the Cerrado have revealed several factors that covary with the structural features of vegetation communities, such as shallow soil nutrient availability (Goodland and Pollard 1973) and disturbance by fire (Moreira 2000). One of the few studies relating the spatial structure of cerrado vegetation to variation in underground changes of soil water was conducted along a catena near a marsh area where vertical distance to a water table was easily measurable (Oliveira-Filho et al. 1989). Results from that study suggested that structural vegetation features covaried primarily with water table depth. Although many of those results have shed some light on the factors that govern structural heterogeneity in the Cerrado, this topic still remains poorly understood.

There is growing agreement that many interacting factors operating at various spatial and temporal scales contribute to the development and maintenance of vegetation patterns in savannas (Silva et al. 2001; Jeltsch et al. 2000). However, soil moisture is frequently recognized as the most important resource affecting vegetation structure and organization in different ecosystems (e.g., Rodrigues-Iturbe et al. 2001). Particularly in savanna ecosystems that are affected by long dry seasons, water from deep soil reservoirs should be a key factor taken into account (Oliveira et al. 2005; Rawitscher 1948). Here we focus on the role of soil water availability and heterogeneity in structuring cerrado communities. In particular, we investigated the linkage between spatial variation of vegetation structural features and plant available water (PAW; soil water content minus the residual soil water content when plants can no longer extract water from the soil). To address this question we determined the spatial distribution of PAW along three 275-m transects through the use of two-dimensional (2-D) geoelectric profiling.

Our approach in this study was to compare the spatial structure of PAW and vegetation properties, at the landscape level, through measurements of spatial autocorrelation on each. Spatial autocorrelation is a property of variables indicating that values, at a given distance apart, are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected by chance. Then, if the spatial autocorrelation coefficients are significant, it means that the studied variable is spatially structured and displays heterogeneity. Otherwise, it displays spatial homogeneity or randomness. Identifying the presence of spatial structure in ecological variables is useful to help understand the mechanisms that organize them. We begin our analysis by describing the spatial structure of PAW over 275-m transects using autocorrelation indices (Moran’s *I*). Once the spatial structure of PAW is established, we describe the spatial structure of the structural vegetation parameters. We took advantage of the measurable spatial structure to investigate possible similarities in the overall patterns, intensity and scales of spatial organization among the vegetation structural parameters and PAW. In addition, spatial patterns in plant distribution were investigated through comparisons with null models. Finally, we also use correlations, with *df* corrected for spatial autocorrelation, to demonstrate several patterns of vegetation structural features with PAW at various soil depths.

Materials and methods

Site description

The study was conducted in a cerrado site located in a protected area [Estação Ecológica de Águas Emendadas (EEAE); 15°34′16.4″S, 47°35′33.4″W] in the center of the Cerrado biome, about 50 km from Brasília. EEAE encompasses a variety of cerrado physiognomies, varying from open grasslands to dense woodlands. Our study was conducted in a typical cerrado locally classified as cerrado stricto sensu (Oliveira-Filho and Ratter 2002). This type of cerrado is dominated by trees and shrubs, but also presents a moderate amount of herbaceous vegetation. It is remarkably dense; in the present study we estimated a local woody plant density of 4,342 plants ha^{-1} and crown cover greater than 40%.

Geomorphologically, EEAE is in a plateau situated at altitudes ranging from 1,000 to 1,300 m above sea level. Hydrologically, the area is characterized by the presence of a well-developed aquifer system (Lousada and Campos 2005). Soils in the region are predominantly clayey, highly weathered Latossolos according to the Brazilian classification system, or Acrustox according to USDA soil taxonomy. The soils are characterized by a high aggregate stability due to the large contents of Fe and Al oxides (Reatto et al. 1998), resulting in well-drained soils in spite of the high clay content. A 22-year record indicates that the mean annual precipitation is 1,453 mm, with 90% of the rain falling between October and March.

Transects

We established three 275-m transects within a cerrado area with no obvious vegetation gradient. The most distant pair of transects were 3,380 m apart. Vegetation measurements were made along these transects and PAW was estimated using soil electrical resistivity measurements performed during the wet (February 2003) and dry season (October 2003).

Soil resistivity surveys have been successfully applied for decades in many realms of science, such as hydrogeology, civil engineering, archaeological prospection and environmental studies (Griffiths and Barker 1993; Tabbagh et al. 2000; Shaaban and Shaaban 2001; Seaton and Burbey 2002; Jackson et al. 2005). Although the volume of water in soil pores is among the dominant factors directly affecting soil resistivity (mineralogy and salinity also have a strong effect, but we assume that they do not vary significantly across our study transects) this technology has not been applied widely to studies of plant–soil water relationships. Here, we used this long-established geophysical tool to estimate PAW and develop an ecological study at the community level.

Estimation of PAW through two-dimensional resistivity profiling

Field resistivity measures were conducted with a commercially available earth resistivity meter (Sting R1 IP single channel memory earth resistivity) connected to a Swift dual mode automatic multi-electrode system (Advanced Geoscience, Tex.). A 56-electrode cable was laid along a straight line transect along the length of the profile (275-m transect) for imaging. For all three transects the electrode separation was 5 m, for a maximum soil resistivity profile depth of about 37 m. The Wenner array configuration was used. The data were inverted using EarthImager 2D software developed by Advanced Geosciences (2004).

Once two-dimensional (2D) resistivity profiles had been constructed, resistivity values for specific soil depths were extracted by applying interpolation and data extraction techniques developed with the GIS software, IDRISI Kilimanjaro version 14-02 (Eastman 2003). The raw inverted resistivity data were saved as universal resistivity data files that were then converted into IDRISI vector files using IDRISI conversion tools. A non-constrained Delaunay triangulation was produced from the vector points of each imaged soil profile using the triangulated irregular network (TIN) model of the GIS software. The TIN facet attributes were then interpolated to generate a raster image from which resistivity values along specific depths were extracted. Resistivity values were extracted at depths of 0, 30, 100 cm and then at each meter up to a maximum depth of 1,000 cm for the 275-m transects. Resistivity data extracted from below 1,000-cm soil depth were discarded because they were beyond the depth surveyed in the calibration of the method (800 cm) or the field observations for textural changes (1,000 cm).

Time domain reflectometry (TDR) was used to calibrate resistivity measurements for estimation of volumetric soil water contents (VWC). The TDR technique relates the apparent dielectric constant of the soil to VWC (Topp et al. 1980). The TDR sensor design, the installation of sensors into soil pits, and the calibration curve developed for Oxisols follows Jipp et al. (1998). Variation in VWC was measured by TDR within three 8-m deep soil pits located along a separate 165-m transect established in the same area at EEAE for calibration studies. At each pit, two vertical TDR sensors were installed at the soil surface to measure VWC in the first 30 cm of soil depth. Horizontal sensors were installed in opposite walls to measure VWC at depths of 50, 100 cm and then at each meter up to a maximum depth of 800 cm. Resistivity measures near each soil pit were compared to VWC obtained through TDR on the same day of the resistivity values. Measurements were taken during the months of January, March, April and September 2002. The regression analyses showed an inverse and highly significant relationship between resistivity and VWC measured by TDR ($r^2 = 0.80$; $P < 0.001$). Based on this regression, we derived a functional relationship [ln(resistivity) = 12.9952 – 0.1913VWC] to convert resistivity values into VWC for the soils of the EEAE study sites.

VWC values were used to estimate PAW, which is the soil water in excess of that held by the soil when roots can no longer extract water. Clay content (60–80%) and bulk density (0.75–0.85 g cm^{-3}) are relatively uniform throughout the profile to 10 m depth at this site (Silva 2003), so water holding properties are expected to vary only modestly as a function of depth. Where soil texture and porosity vary more widely with depth, vertical variation in water-holding properties may be more distinct and could be an important consideration when applying this method to such soils. Although these properties are less variable in the present study, some vertical variation is still possible, and the ability of roots to access this water may also vary vertically. For these reasons, we found that it was necessary to use different functions for calculating PAW for the 0- to 400-cm depth segment and lower depth segments:

$$\mathrm{PAW}_{0-400\,\mathrm{cm}} = \mathrm{VWC} - \mathrm{VWC}_{\mathrm{min}} \tag{1}$$

$$\mathrm{PAW}_{400-1000\,\mathrm{cm}} = \mathrm{VWC} - \theta r \tag{2}$$

where VWC is the volumetric water content obtained for that soil depth through resistivity measurements and calibration with TDR measurements; $\mathrm{VWC}_{\mathrm{min}}$ (0.13 $\mathrm{cm}^3\ \mathrm{cm}^{-3}$) is the lowest volumetric water content observed at each depth above 400 cm in our data set; and θr (0.19 $\mathrm{cm}^3\ \mathrm{cm}^{-3}$) is the residual water content estimated by Silva (2003) for the deep soil horizons of our study site by fitting data from water retention curves to the van Genuchten (1980) soil moisture function, using a nonlinear estimation procedure that minimizes the sum of squares error of the model:

$$\theta h = \theta r + (\theta s - \theta r)\left[\frac{1}{1 + (\alpha\,|h|)^{n}}\right]^{\left(1-\frac{1}{n}\right)} \tag{3}$$

where θh is the VWC at a given matric potential h, θs is the saturated VWC, and α and n are fitting parameters (kPa^{-1} and no unit, respectively).

To derive the van Genuchten parameters, Silva (2003) obtained undisturbed soil cores from the calibration soil pits of our study site, re-wetted them to saturation, and then sequentially centrifuged them to apply a range of matric potentials of –0.007, –0.010, –0.033, –0.101 and –1.520 MPa (Silva and Azevedo 2002). After each centrifuging cycle, soil samples were weighed to determine the remaining water at each soil water potential. The parameter fitting process requires starting with initial values for each parameter, using the average van Genuchten parameters reported by Hodnett and Tomasella (2002) for tropical clay soils. The parameter estimates are then improved by successive iterations obtained with an optimization algorithm applied through the Solver tool (Microsoft Excel) using the data from the water retention curve.

The van Genuchten model could not be applied to the top 400 cm because field observations of VWC measured by TDR and soil resistivity were often lower than the calculated van Genuchten θr values calculated for those depths, perhaps because the vegetation in this seasonally dry biome is well adapted to drawing VWC to values below the lowest laboratory measured matric potential (–1.52 MPa) used to fit the van Genuchten model. Below 400 cm soil depth, the observed values of VWC were consistently at or above the van Genuchten estimates of θr, thus permitting us to use Eqs. 2 and 3.

Based on the behavior of raw resistivity values and observations of soil water holding properties, PAW was summed for intervals of 0- to 400-, 400- to 700-, and 700- to 1,000-cm depths. For the statistical analysis, mean PAW values for 20-m-long horizontal segments of the transects were paired with vegetation-respective inventory plots along the transect (described below), which were 10 m × 10 m. The PAW values were averaged over a longer segment of the transect than the vegetation plot (extending 5 m on either side of the vegetation inventory plot) because it was assumed that stems within a 10 × 10-m plot might obtain water from roots that extended beyond the boundaries of the plot.

Vegetation measurements

Vegetation was surveyed within the three 10 × 275-m transects excluding a 55-m area at the borders of each resistivity sampling transect, for a total sampled area of proximately 0.22 ha/transect. All woody plants (trees and large shrubs) ≥2.86 cm diameter (9 cm circumference) at 0.3 m from ground level were included. Plants inside the plots were mapped, permanently tagged and identified to species. For each tagged individual, we measured height, basal circumference (at 0.30 m height), crown depth and individual crown major and minor axes. Crown depth was obtained by the difference between plant height and height of the lowermost foliage level. Canopy volume of individual plants was calculated as an ellipsoid. We did not attempt to calculate biomass directly, due to a lack of reliable allometric equations that are appropriate for the broad range of plant architectures for the diverse species of the Cerrado. We calculated the sums of height, basal area, basal area × height, crown depth and crown volume per plot, which we use as proxies for plot biomass. While average values per plot are independent of plant density, the sums include the combined effects of density and architecture.

In each transect we computed leaf area index (LAI) through hemispherical photographs taken at 0.40 m height, every 10 m. Photographs were taken at one time in the dry season (July 2002) and two different times in the wet season—February 2003 (near the end of the wet season) and December 2003 (mid wet season). We used a leveled Nikon fish eye lens with 180° field of view mounted on a Nikon Coolpix 950 camera. The software Gap Light Analyzer version 2.0 was used to compute LAI.

Statistical analysis

Vegetation attributes were first characterized with descriptive statistical analysis using the statistic routine in Sigma Plot for Windows version 9.01.

To determine how spatial variation in plant attributes was related to underground distribution of PAW, the first step was to characterize the spatial structure of PAW. Moran's *I* correlograms and semivariograms were both used to evaluate spatial patterning of PAW; however, only Moran's *I* analyses are reported because Moran's *I* correlograms provide accessibility to a significance statistical test. By applying Moran's *I* coefficient we are measuring spatial correlation by evaluating the similarity between samples of PAW or vegetation attributes as a function of spatial distances (Legendre and Legendre 1998). Moran's *I* coefficient usually varies between –1 and 1 for maximum negative and positive autocorrelation, respectively, although values lower than –1 or higher than +1 may occasionally be obtained (Legendre and Legendre 1998). Moran's *I* values significantly different from zero indicate similarity (for positive coefficients) or dissimilarity (for negative coefficients) higher than expected by chance. We partitioned spatial distances along the resistivity transects into seven intervals (20, 40, 60, 80, 110, 140 and 210 m). Distance classes were defined by maximizing the similarity in the number of pairs of observations, which varied from 27 to 47 pairs. This criterion provided the same power across all distance classes in the tests of significance (Diniz-Filho et al. 2003). Correlograms were constructed by plotting Moran's *I* coefficient as function of spatial distance. The correlogram as a whole was considered significant ($\alpha \leq 0.05$) by applying the Bonferroni criterion (Legendre and Legendre 1998), that is, when at least one of its coefficients was significant at α/k, where k is the number of distance classes. Spatial patterning in vegetation attributes were evaluated using only Moran's *I* analysis. Moran's *I* coefficients through correlograms were also used to compare spatial variation in PAW with spatial variation in plant attributes. Spatial analyses were performed using the software Spatial Analysis in Macroecology version 1.1 (Rangel et al. 2005).

The scale-dependent spatial variation in plant density was analyzed by comparing the observed distribution of density (measured at a range of spatial scales) against a null model of spatial pattern that assumes a random distribution of individuals within each transect. We used 6,000 Monte Carlo simulations (Metropolis and Ulam 1949) to generate random permutations of the distribution of individual trees along each transect and sub-divided the 2,750-m^2 transects into sample plots varying from 50 to 500 m^2. For all simulations, the total number of individual trees within each transect was conserved. Patterns from our simulations provided a null model for the spatial variance in density arising from individual trees that are distributed according to a random spatial process within the transect. By comparing observed spatial variance in the density of individuals to the ranges of simulated spatial variance in density, we were able to determine if the observed patterns were significantly non-random within each transect. Significance of observed spatial patterns in tree density was determined by comparing the observed spatial variance with the range of values obtained from the simulated spatial pattern analysis (Caylor et al. 2003). Observations of variance in density greater than the 95% confidence interval obtained from the Monte Carlo simulations indicated the presence of significant spatial patterns within the observations at each spatial scale of analysis.

In order to complement Moran's *I* analysis, Pearson's correlation analyses were conducted to quantify the strength of association between PAW and plant attributes. As the presence of spatial autocorrelation in the variables can inflate the type I error of classical statistical tests of significance, the *df* were corrected by Duttilleul's modified correlation test (Legendre et al. 2002) using Spatial Analysis in Macroecology version 1.1 (Rangel et al. 2005). This analysis was done whenever Moran's *I* test demonstrated clear spatial autocorrelation in the variables investigated. Vegetation attributes used for correlation analysis were expressed as an average value or the total sum per 100-m^2 plot. The average values represent individual plants in the plots, whereas the sums add the effect of plant density and serve as approximate proxies for the total biomass in the plots.

Results

Vegetation structure

Descriptive statistics for each vegetation attribute are shown on Table 1. No major difference in the averages of plant density, plant height, basal area, crown depth and crown volume was observed among transects. Plant density varied from 31 to 71 plants per 100 m^2. Frequency distributions showed that the three transects had the highest proportion of plants represented in the height classes between 0.80 and 3.30 m and diameter classes between 2 and 8 cm diameter (Fig. 1). A wide range of LAI (0.3–1.8; Table 1) and percent of canopy openness (20–60%) was observed along the three transects. Hereafter, transects 1, 2 and 3, are referred to as T1, T2 and T3, respectively.

Spatial patterns of PAW

There were clear differences in the soil water availability among the three transects (Fig. 2). The highest PAW

Table 1 Descriptive statistics for structural vegetation attributes in the three 10 × 275-m transects studied in Águas Emendadas Ecological Station (Brazil). *CV* Coefficient of variation, *Min–max* minimum–maximum, *LAI* leaf area index

Attributes	Transect 1	Transect 2	Transect 3
Plant density (no./100 m^2)	(*n* = 22)	(*n* = 22)	(*n* = 22)
Min–max	31–71	28–61	33–63
Median	46	45	42
Mean	47	43	43
Plant height (m)	(*n* = 1,035)	(*n* = 950)	(*n* = 953)
Min–max	0.40–10.00	0.30–10.50	0.39–12.00
Median	2.00	1.90	2.30
Mean	2.32	2.24	2.57
Basal area (cm^2)			
Min–max	6–1184	6–748	6–1108
Median	20	20	24
Mean	48	48	49
Crown depth (m)			
Min–max	0.05–6.56	0.05–5.10	0.05–6.50
Median	1.03	0.80	1.05
Mean	1.27	1.08	1.27
Crown volume (m^3)			
Min–max	0.020–2606	0.008–2064	0.004–2994
Median	8.80	4.42	7.51
Mean	43.89	43.34	38.09
LAI	(*n* = 22)	(*n* = 22)	(*n* = 22)
LAI July (2002)			
Min–max	0.33–1.23	0.36–1.84	0.44–1.38
Median	0.86	0.88	0.73
Mean	0.80	0.95	0.79
CV (%)	33	42	28
LAI February (2003)			
Min–max	0.39–1.35	0.44–1.41	0.50–1.42
Median	0.81	0.89	0.88
Mean	0.85	0.93	0.87
CV (%)	29	27	26
LAI December (2003)			
Min–max	0.44–1.14	0.48–1.66	0.61–1.42
Median	0.81	0.90	0.87
Mean	0.83	0.92	0.87
CV (%)	21	30	23

values were frequently observed for T3, contrasting with the lowest for T2. Intermediate PAW values were observed for T1. The deeper soil in T2 showed very dry areas at the beginning of the transect, and then PAW increased continuously from 0 to 275 m horizontally along the transect. At the end of T2, similar or even higher PAW values than in T3 were found. Such spatial variation was also observed in T1 but it was less pronounced (Fig. 2).

Moran's *I* correlograms revealed clear spatial autocorrelation of PAW in all three transects; however, the strength of the autocorrelation differed among them (Fig. 3). T3 presented the weakest spatial autocorrelation, where correlograms were frequently not significant. T1 and T2 showed significant correlograms for all soil depths intervals, in both seasons, but the strongest spatial autocorrelation was observed in T2. Positive spatial autocorrelation was found at up to 20 m horizontal distance in the upper soil compartment of T2 and up to 60 m horizontal distance in the deeper soil compartments (Fig. 3). Significant negative autocorrelation was also observed for long distances. The shape of the correlogram for the depths below 400 cm in T2, with a monotonic decrease in PAW (Fig. 3) is compatible with a linear gradient (Legendre and Legendre 1998). Linear gradients are commonly revealed by significant positive autocorrelation over short distances coupled with significant negative autocorrelation over long

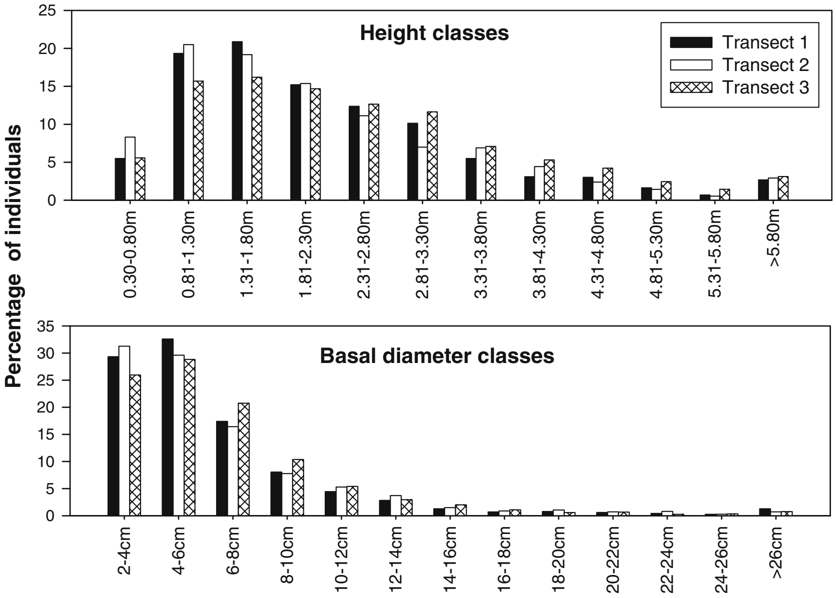

Fig. 1 Classes of plant height and basal diameter of woody plants (trees and large shrubs) for the three transects studied in Águas Emendadas Ecological Station (Brazil). $n = 1{,}035$ plants in transect 1, $n = 950$ plants in transect 2, $n = 953$ plants in transect 3

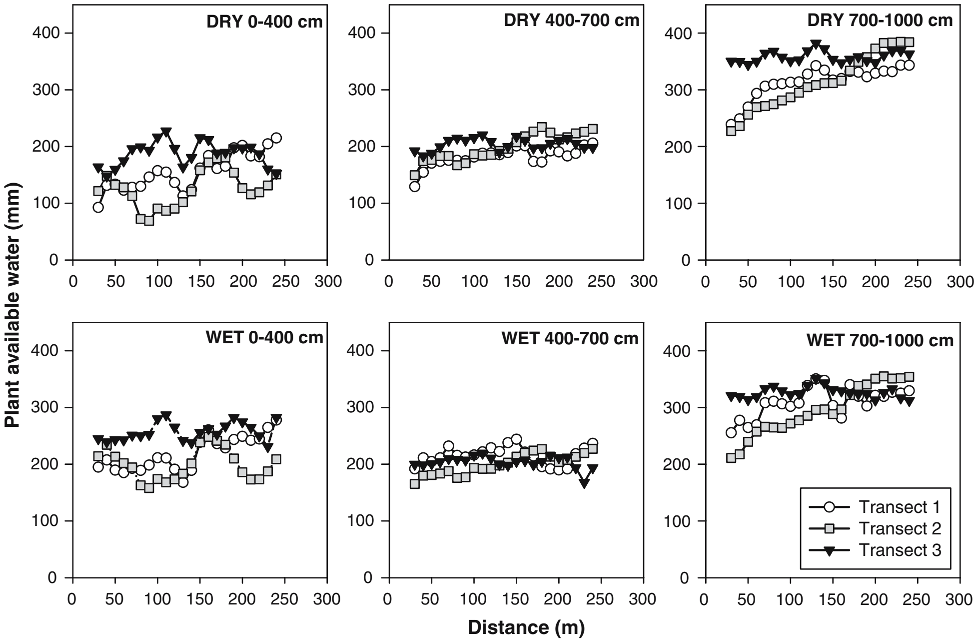

Fig. 2 Plant available water distribution along the three 275-m transects in Águas Emendadas Ecological Station during the dry (*DRY*; October 2003) and wet season (*WET*; February 2003). Values of plant available water were summed for intervals of 0- to 400-, 400- to 700-, and 700- to 1,000-cm depths

distances (Diniz-Filho et al. 2003). T1 presented positive spatial autocorrelation in PAW, particularly in the upper soil compartment, for which a spatial structure compatible with a linear gradient was also observed (Fig. 3). Overall, the three transects were in the following order of soil water availability: T3 > T1 > T2. The inverse order was observed in terms of soil water heterogeneity: T2 > T1 > T3.

Spatial patterns of vegetation attributes

Along T1 and T3, Moran's *I* coefficients were frequently non-significant (data not shown) and none of the correlograms showed global significance. Therefore, clear trends were not observed for these transects, indicating weak spatial structure in the vegetation attributes. By contrast, T2 showed significant spatial autocorrelation for all density-dependent vegetation attributes investigated (Fig. 4), for which all correlograms were globally significant, except LAI in February and December. Plant density along T2 showed positive spatial correlation up to 40 m distance, while the other plant attributes—sum of height, sum of basal area, sum of basal area × height, sum of crown volume and seasonal measurements of LAI (Fig. 4)—showed significant positive spatial autocorrelation up to 20 m.

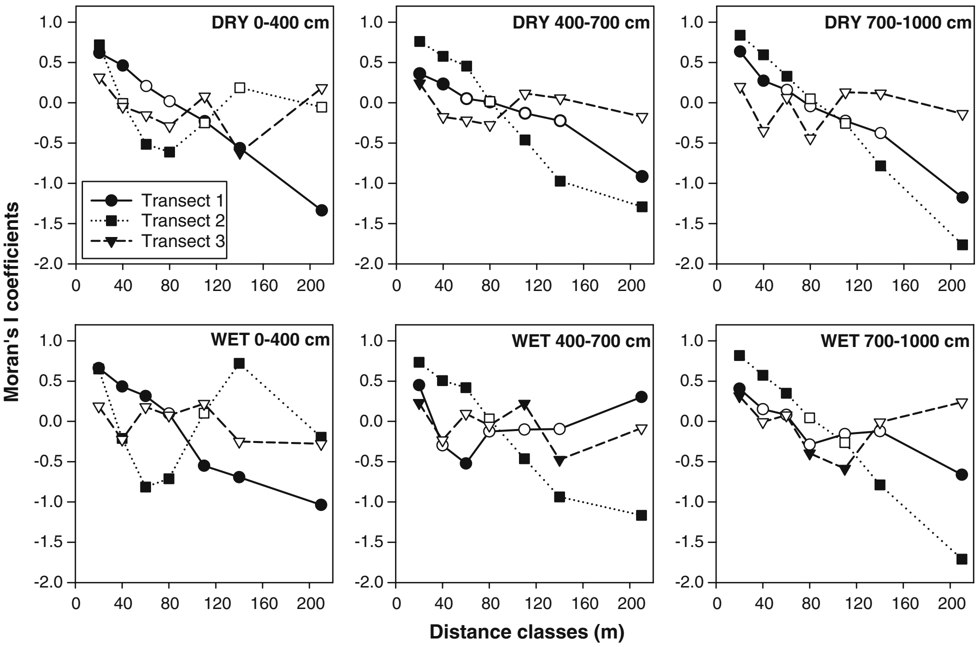

Fig. 3 Moran's spatial correlograms for plant available water along the three 275-m transects in Águas Emendadas Ecological Station. Distance classes were defined by maximizing the similarity in the number of pairs of observations (n = 27–41). *Closed symbols* indicate significant Moran's *I* ($P < 0.05$) and *open symbols* non-significant Moran's *I*

Negative spatial autocorrelation was also observed for all vegetation attributes along T2 at distances close to 60–80 m (Fig. 4). Overall, most vegetation attributes along T2 showed a similar spatial structure with spatial scales at 20 m and 60–80 m. In contrast to the significant spatial structure for density and the density-dependent sums of vegetation attributes along T2, a clear spatial structure could not be found for the means of vegetation parameters per plot for any of the three transects.

Comparisons of spatial structure of PAW in the upper soil compartment (0–400 cm), for the dry season, with different vegetation attributes in T2 are presented in Fig. 4. A striking similarity exists between pairs of correlograms for PAW and vegetation attributes. The vegetation attributes showed spatial variation at similar scales to those observed for PAW (particularly at 20 m and 60–80 m). Spatial variation patterns in T2 for LAI and sum of height closely matched those for PAW, whereas sum of basal area, basal area × height, and plant density were less well matched (Fig. 4). Particularly, sum of height showed a pattern in the spatial structure with scales perfectly corresponding to those for PAW (Fig. 4). The correspondence of the spatial structure of vegetation attributes with PAW supports the notion that the spatial structure previously reported here does not simply correspond to spatial autocorrelation, but, very likely, that vegetation attributes and PAW are covarying (spatial dependence).

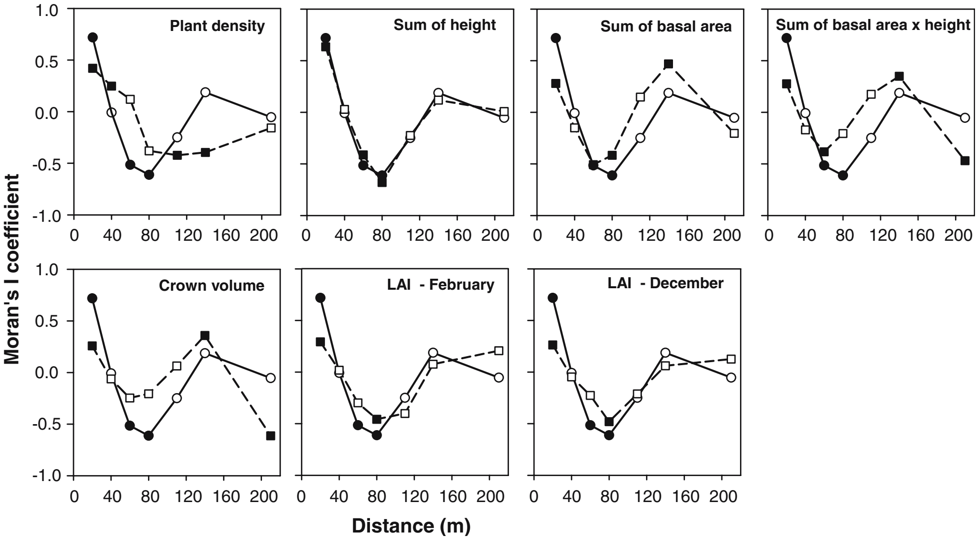

Fig. 4 Moran's spatial correlograms for plant available water and structural vegetation attributes for transect 2 in Águas Emendadas Ecological Station. *Solid lines* represent plant available water at 0- to 400-cm depth for the dry season and *dashed lines* represent the vegetation attributes. *Closed symbols* indicate significant Moran's *I* ($P < 0.05$) and *open symbols* non-significant Moran's *I*

Plant distribution through comparisons with null models

Figure 5 shows the trends of expected and observed patterns of density variance along each transect assuming that expected plant densities are randomly distributed. Observed plant density variance outside the confidence intervals indicate departure from the null hypothesis of complete spatial randomness and, therefore, the presence of a spatial pattern associated with a specific spatial scale.

Comparison of plant density distribution of observed and expected data revealed striking differences among the three studied transects (Fig. 5). Observed plant density variance values along T3 always fell around the expected values and inside the confidence intervals, irrespective of the scale, indicating random distribution. By contrast, observed values of plant density variance along T2 fell outside the upper confidence interval, clearly suggesting an aggregated pattern (contagious or clumped distribution) across a range of spatial scales (Fig. 5). T1 showed some aggregation, but it was not as consistent as that observed for T2. These results show us that despite relatively similar means for all structural parameters (Table 1), the three transects exhibited markedly different patterns of plant distribution. T2 showed plants highly aggregated, T1 plants slightly aggregated, while T3 did not show any pattern, indicating that plants were randomly distributed over the space.

Correlations between vegetation structure and PAW

The correlograms shown in Fig. 4 were a robust means of demonstrating the spatial covariation of vegetation structural features with the PAW of soil at a depth of 0–400 cm in T2. Here, we have complemented the spatial analyses with correlation analyses to describe quantitatively the rate of change of vegetation attributes with changes in PAW. The other transects and other soil depths were also included in these analyses.

Simple correlation analyses and correlations corrected for spatial autocorrelation are shown in Table 2. The significance of several simple correlations was maintained after autocorrelation was taken into account. Where a strong spatial structure in PAW was detected, however, correlation coefficients were frequently not significant, such as observed when the averages for T2 were used (Table 2). The lack of significant corrected correlations for most attributes in T2 means that either spatial autocorrelation have inflated type I errors in the simple correlations or that the modified Duttileuls's test did not have enough power to detect the correlations. As discussed by Legendre et al. (2002), the presence of strong spatial dependence

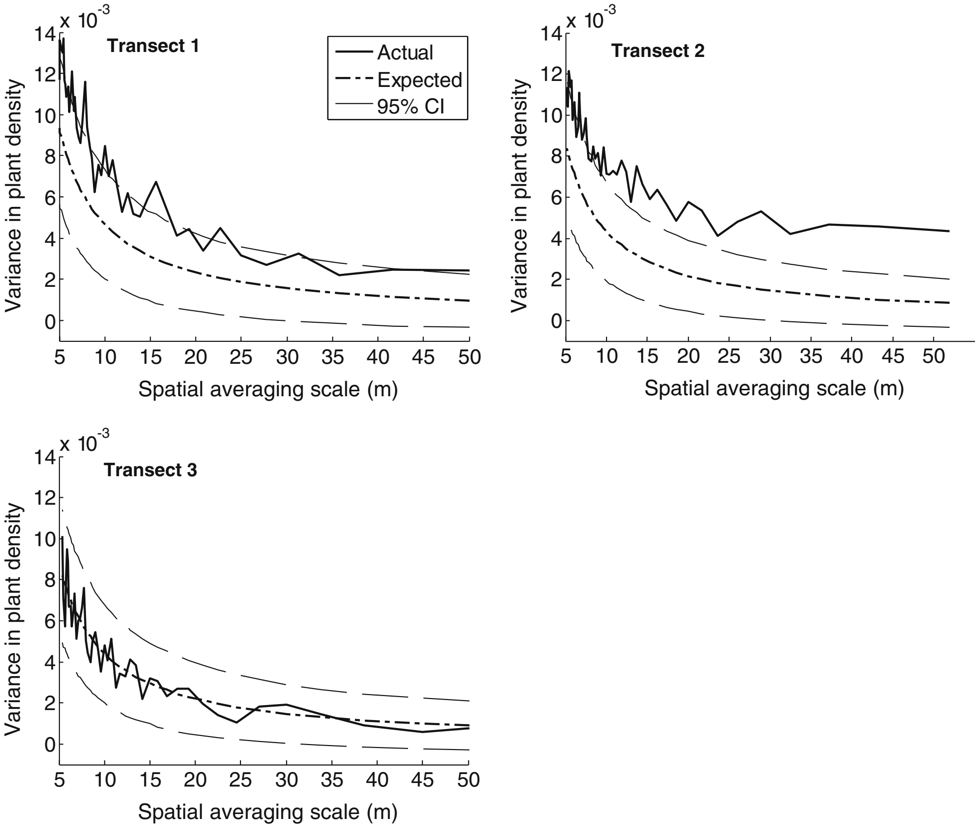

Fig. 5 Spatial pattern of plant density variance across a range of spatial scales along the three 275-m transects in Águas Emendadas Ecological Station

may reduce the power of the modified test, particularly in small sample sizes. Therefore, we have opted to present all significant simple correlations (including those not significant after controlling for autocorrelation), although they should be interpreted as indicators only. To assure further the validity of correlation results presented, we also performed regression analyses and checked for autocorrelation of the residuals. For this purpose, we assumed the vegetation attributes as the response variable and PAW as the explanatory variable. In all cases, the Durbin–Watson *D*-statistic was not significant, indicating weak or no autocorrelation of the residuals.

As expected from the spatial relationships found between density-dependent vegetation features and PAW at 0- to 400-cm soil depth in T2, plant density in that transect was significantly and positively related to PAW in this soil compartment, in both seasons (Table 2; Fig. 6). Also, strong correlations were found for sum of height ($r = 0.88$) and sum of crown depth ($r = 0.60$). In contrast to the positive relationships with the upper soil in T2, the within-plot averages of plant height, basal area, basal area × height, crown depth and crown volume were significantly and negatively correlated with PAW at deep depths (below 400 cm; Table 2). Significant correlation coefficients varied from –0.43 to –0.72. Correlations were observed in all three transects, although T3 only showed significant relationships for the crown attributes (crown depth and volume). Overall, we observed a convergent

Table 2 Significant Pearson's correlation coefficients for the relationships between structural plant attributes[a] and plant available water in the wet (February 2003) and dry season (October 2003)

Plant attributes	Dry season			Wet season		
	0–400	400–700	700–1000	0–400	400–700	700–1000
Mean height						
Transect 1		**–0.534****			**–0.684*****	
Transect 2			–0.455*			–0.432*
Mean basal area						
Transect 1		**–0.566****				
Transect 2			–0.521**			–0.508**
Mean basal area × height						
Transect 1		**–0.604*****	**–0.426****			
Transect 2			–0.553***			–0.551***
Mean crown depth						
Transect 1			**–0.436***		**–0.571****	**–0.445***
Transect 2		–0.588**	–0.664***		–0.560**	–0.627**
Transect 3		**–0.518****				
Mean crown volume						
Transect 1		**–0.551****	**–0.536****		**–0.558****	**–0.533****
Transect 2		–0.640***	–0.718***		–0.573**	–0.712***
Transect 3		**–0.431***				
Plant density						
Transect 2	**0.672*****	0.618**	0.471*	**0.502***	0.635***	0.476*
Sum of height						
Transect 2	**0.884*****	0.498*		0.820***	0.535**	
Sum of crown depth						
Transect 2	**0.605****			0.637**		
Sum of crown volume						
Transect 1		**–0.454***			–0.433*	
LAI						
February 2003						
Transect 1	0.426*			0.440*		
Transect 2				0.464*		
Transect 3	**–0.454***					
December 2003						
Transect 1	0.465*			0.448*		
Transect 2	0.535*			0.574**		

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Numbers *in bold* are also significant ($P < 0.05$) after correcting the *df* by spatial autocorrelation estimation with Duttilleul's modified *t*-test

[a] Vegetation structural attributes are represented as means or sums for 100-m^2 plots

pattern in the Pearson's *r*-values using averages among the three transects; they were negative and significant with the deep soil (400–700 and 700–1,000 cm; Table 2). LAI in February 2003 (wet season) for T3 was negatively correlated with PAW measured in the subsequent dry season (October 2003) (Table 2). All correlations between LAI in the wet season and PAW were found for the upper soil compartment. Correlations in T1 and T2 were always positive and present in both seasons, contrasting to the negative correlation found for T3 only in the dry season.

Discussion

Our study has exposed the strong spatial heterogeneity at a fine scale associated with PAW in the study area (Figs. 2, 3). We observed large spatial variation of PAW at both the landscape scale (variation among the three transects) and the local scale (within each 275-m transect). The analysis of spatial patterns of PAW revealed that this variability was frequently spatially structured. Most importantly, the three transects differed with respect to the spatial pattern of PAW (Fig. 3). These distinct patterns of soil water availability and heterogeneity provided us with a unique opportunity to explore links between vegetation structural properties and PAW at the landscape level. Up until now, studies exploring spatial covariation of PAW and vegetation structure have not been developed in savannas. Our study area did not show any obvious vegetation gradient and the subtle spatial patterns were only revealed after the spatial analysis. This situation differs, for example, from those reported by Oliveira-Filho et al. (1989) where a clear variation in physiognomy was found in a landscape characterized by a strong slope.

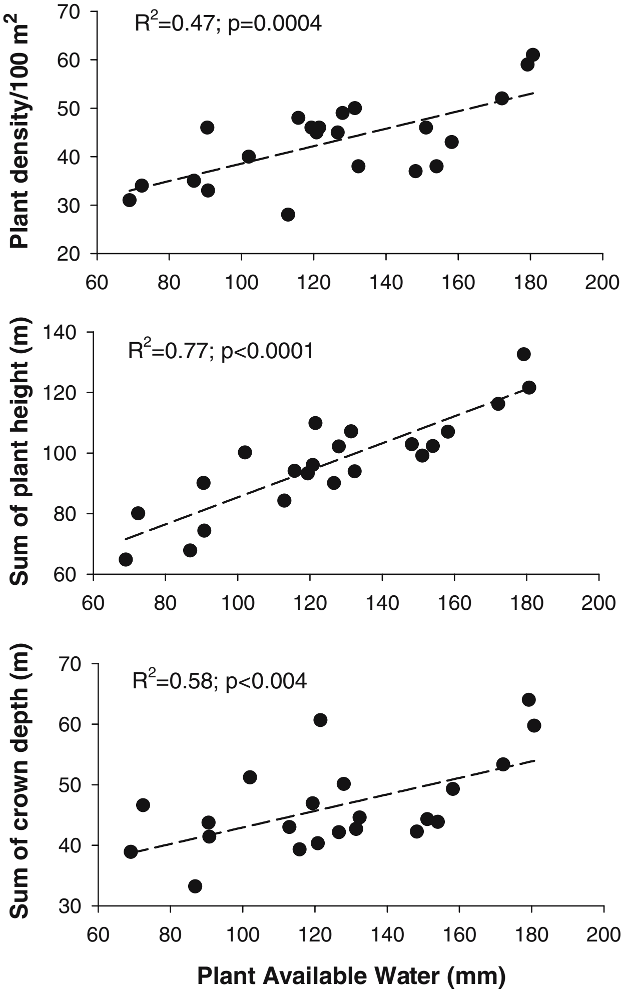

Fig. 6 Relationship between some vegetation attributes and plant available water in the 0- to 400-cm soil interval, during the dry season (October 2003), for transect 2 at Águas Emendadas Ecological Station

Our results revealed congruence between the community spatial arrangement and the spatial heterogeneity in PAW. Co-organization is firstly evident from the overlap in the patterns and scales of the spatial variation in PAW and attributes representing the plot (LAI and total sum of each measured vegetation attribute) along T2 (Fig. 4). In particular, the spatial variation of sum of heights was nearly identical to the spatial pattern of the PAW at 0- to 400-cm depth in the dry season. Assuming that the vegetation is organized according to PAW heterogeneity, this soil depth interval would be the most directly related to vegetation structural features. Apparently, the seasonal water demand is met largely by uptake from this soil depth.

The second piece of evidence of co-organization between PAW and vegetation structure is the spatial pattern of plant distribution coupled with PAW heterogeneity in the three transects (Fig. 5). The greatest heterogeneity in PAW, found for T2, was coupled with the highest degree of plant aggregation. By contrast, the lower heterogeneity in PAW along T3 was coupled with randomness in plant distribution. T1 exhibited an intermediate PAW heterogeneity and relatively weak plant aggregation. Plant spatial arrangement in communities is usually not random, presenting spatial patterns at several scales (Dale 1999). Aggregation was the most frequent plant distribution pattern observed in arid/semi-arid savannas in the Kalahari region, irrespective of the wide range of annual precipitation (Caylor et al. 2003). A clumping pattern of the community was also reported in a savanna of the South American Llanos, in Venezuela (San José et al. 1991).

Several mechanisms are associated with plant distribution patterns in plant communities, such as resource distribution (Dale 1999), disturbance (Higgins et al. 2000), herbivory (Weber et al. 1998) and dispersal mechanisms (Kunstler et al. 2004). In our study, we observed random patterns in plant distribution associated with lower heterogeneity and higher levels of water resource. The relatively low heterogeneity in the 0- to 400-cm soil compartment in T3 (Figs. 2, 3) suggests that there are no preferential niches for colonization. By contrast, the strong aggregation in T2, the driest and most variable of the three transects, provided evidence for colonization in optimal establishment patches, where soil water is more abundant. These three neighboring areas do not have a recent history of disturbance by fire, and they show relatively similar species composition (J. N. Ferreira, unpublished data) and, thus, relatively similar dispersal patterns are expected. Therefore, the contrast in the spatial patterns observed is consistent with the hypothesis that PAW heterogeneity is an important structuring factor in plant distribution in these areas.

The correspondence in the spatial patterns between PAW and vegetation could only be found for the summed attributes, which combine the effects of plant density and individual architecture. Furthermore, spatial covariation of vegetation structure and PAW was only detected for T2, where a strong degree of aggregation was observed. Because no clear patterns of plant aggregation were observed for T1 and T3, a clear spatial pattern in the vegetation attributes was not observed across these transects. The spatial covariation of the total sum per plot of vegetation attributes (i.e., height, basal area and crown depth) found for T2, appears to be related to plant aggregation, given that no clear spatial structure was observed for the averaged attributes. These results draw attention to plant density and distribution as the primary structural features associated with PAW.

Correlation analysis revealed the nature of the covariation between PAW and vegetation attributes reported above. The aggregation pattern observed in T2 seems largely determined by the presence of niches with higher plant water availability. The positive relationship between plant density and PAW along T2 reinforce the importance of soil moisture in the recruitment and establishment success in this ecosystem affected by pronounced dry periods. A positive relationship of establishment success and soil moisture was demonstrated for two artificially irrigated cerrado species (Hoffmann 1996). The trend of increasing LAI with PAW along T2 (Table 2) suggests a further positive relation of woody plant density with soil water availability. Although many cerrado shrubs and trees propagate vegetatively, sexual reproduction and seedling establishment are not only very common, but also involve mechanisms which are well adapted to the climatic conditions (Oliveira 1998). The initial establishment phase is critical for seedlings of woody plants in savanna ecosystems due to the competition for light and water with the grass layer. Hoffmann (1996) demonstrated that success in seedling establishment of nine cerrado species out of 12 increased with woody cover.

Average values for all vegetation attributes were consistently and negatively correlated to the PAW in deeper soil layers (below 400 cm), across the three transects (Table 2). This pattern is consistent with two plausible interpretations: (1) more PAW in deep soil is associated with plants with smaller aboveground dimensions, or (2) plants with taller architectures are depleting the soil water more at deeper depths. Concerning the first possibility, if roots are accessing deeper soil layers because more soil water is available there, this may compromise the investment in aerial biomass, thus changing the shoot/root ratio. Additionally, the development of deeper roots may be driven by the higher plant density in the wetter sites, which implies stronger competition aboveground and belowground. However, assuming that our results are mainly related to plant density in the stands, much stronger correlation coefficients would be expected in T2 compared to the other two transects. Instead, we have observed a relatively similar pattern of negative correlations between deep soil PAW and mean vegetation attributes among three of the transects.

The second plausible explanation for the negative correlations between averaged aboveground attributes and deep soil PAW could be water use by vegetation, where plants of greater height, basal area, crown depth and crown volume would be drawing more soil water at deeper depths than plants of smaller stature. A large range in size is observed among the species found in our area (Table 1). While most plant species show an average height of around 2–3 m, a few of them can reach 10–12 m height and a crown volume more than 40-fold higher than the average. This variation in size, either related to the life form (shrubs or trees) or to the intrinsic interspecific variations, may imply differences in the water demand and also in the depth of water uptake. Rooting depth, as well as lateral root spread, is expected to increase with canopy size, most likely because larger plants need more roots to supply a greater leaf area with resources. Hence, trees are expected to show deeper rooting depths than shrubs (Schenk and Jackson 2002). The relationship between aboveground biomass and water transport was demonstrated by Meinzer (2003) who found convergent patterns in these aspects regardless of the species identity. Other studies of cerrado species have revealed relationships between water relations and a number of aspects such as phenological group (Jackson et al. 1999) and wood density (Bucci et al. 2004). Relationships with plant aboveground dimensions, however, have not yet been explicitly investigated.

These lines of evidence support the hypothesis that the negative correlations of the aboveground attributes with the deeper soil layers are related to water uptake patterns by plants. To build a more complete picture related to this pattern, however, other physical and biological aspects that influence community structure should be taken into account. Some of these aspects are soil water dynamics among the different soil compartments, deep versus shallow root functioning, trade-offs between aboveground and belowground resource allocation, and interactions among neighbors, including competition for space.

Our study has demonstrated the feasibility of using the 2D soil resistivity profiling technique to estimate PAW. Compared to other methods currently used in ecological studies (Rundell and Jarrell 1991), this technique has the advantages of estimating soil water at broad spatial scales and deeper depths. Also, unlike usual methods, it does not require any digging or destructive sampling (Tabbagh et al. 2000). Although our study covers a particular type of biome (tropical savannas), the technique has the potential to be applied in a broad variety of environments. The sampling intervals between resistivity probes, and hence the vertical and horizontal dimensions of the 2D images, can be varied to meet different survey purposes with varying resolutions of scale. The 2D resistivity profiling technique, as the approach developed here, may open new avenues to ecologists investigating vegetation and soil water relationships.

Conclusion

These findings provide insights for understanding the mechanisms associated with vegetation patterns in the savanna of this study site. Our results suggest strong co-organization between vegetation structure and PAW heterogeneity at the scale of tens of meters, supporting the hypothesis that soil water is a dominant factor among many interacting forces regulating vegetation patterns of these communities. Plant density and spatial distribution emerged as key factors associated with the PAW contrasts among transects. A positive relationship between plant density-dependent structural attributes of the vegetation and PAW of the top 400 cm of soil along one of the transects suggests an important role of soil water resources in the establishment and recruitment success in this ecosystem affected by pronounced dry periods. Furthermore, our results are consistent with water depletion by plants down to 10-m depth, which seems to be influenced by the presence of individual plants of large stature in the plots. Our results support the hypothesis that structural features of vegetation in these savannas are largely influenced by the soil water in the first few meters of the soil, while the vegetation architecture itself also influences soil water availability in the deeper soil layers. Finally, the results presented here demonstrate the great potential of the 2D resistivity profiling technique for plant ecology studies.

Acknowledgements The A. W. Mellon Foundation provided financial support for this effort. CNPq provided a fellowship to the first author. The efforts of E. A. Davidson and M. Bustamante were also partially supported by NASA grant NNG06GD51G as part of the LCLUC program. D. C. Garcia-Montiel was supported by the PVE/Capes program. We are grateful to Carlos Klink and Liliane Bezerra for providing the TDR data and infrastructure. We thank Dr Euzebio M. da Silva of EMBRAPA Cerrados for analyses of water retention curves and for assistance with data interpretation. We thank Frederick Meinzer, Andy Bunn, and Moacyr Dias-Filho whose comments helped to improve this paper. Discussions with Mario Fariñas, supported by IAI project CNR 40, contributed greatly in an early stage of the analysis. Luiz Solórzano provided support during the initial phase of this research. We are grateful to Pedro Simpson-Junior, Danielle Matias, Cesar Luiz Prado, Marcos Soares, Elisa Brusi and Moara Pedrosa for valuable field assistance. We also thank the administration of Estação Ecológica de Águas Emendadas and the Programa de Pós-graduação em Ecologia of the University of Brasília for logistic support.

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