Functional Ecology 2005 **19**, 574–581

Deep root function in soil water dynamics in cerrado savannas of central Brazil

R. S. OLIVEIRA,*†‡ L. BEZERRA,* E. A. DAVIDSON,§¶ F. PINTO,* C. A. KLINK,*§ D. C. NEPSTAD§¶ and A. MOREIRA**

*Departmento de Ecologia, Universidade de Brazilia, CP 04631, Brasília, DF, 70919-970, §Instituto de Pesquisa Ambiental da Amazônia, Brazilia, DF, 70865-530, Brazil, ¶Woods Hole Research Center, PO Box 296, Woods Hole, MA 02543, and **World Bank, Washington, DC, USA

Summary

1. Water is a key resource in tropical savannas. Changes in vegetation structure due to land-use change and increased fire frequency may affect the availability of water and the flux of water through these ecosystems.

2. We compared the seasonal soil moisture dynamics of two adjacent savanna ecosystems with contrasting tree densities in central Brazil. Our goal was to investigate the influence of tree density on deep water uptake, soil water dynamics and evapotranspiration.

3. Soil water was measured using a depth of 7.5 m beneath the tree-dominated *cerrado denso* ecosystem and to 4 m beneath the grass-dominated *campo sujo* ecosystem. Plant-available water (PAW) throughout the *cerrado denso* soil profile ranged from 293 mm at the end of the dry season to 689 mm during the wet season. In the grass-dominated site, PAW in the profile ranged from 155 to 362 mm.

4. During the dry season, \approx 82% of the water used in *cerrado denso* and 67% in *campo sujo* was extracted from the profile below 1 m. The tree-dominated *cerrado denso* used 137 mm more water than the grass-dominated *campo sujo*. Significant deep soil water uptake was also observed during the wet season of 1998, when rainfall was below average. **5.** Evapotranspiration (ET) rates (estimated as change in soil moisture over time) were higher in *cerrado denso* than in *campo sujo* during both seasons. Estimated ET ranged from 1.4 mm day⁻¹ during the dry season to 5.8 mm day⁻¹ for the wet season in *cerrado denso*, and from 0.9 mm day⁻¹ in the dry season to 4.5 mm day⁻¹ in early wet season in *campo sujo*. The differences in PAW and ET rates between the two ecosystems are associated not only with differences in root distribution, but also with differences in tree densities and the phenology of full-leaf canopies.

6. Our results suggest that deep-rooted plants may contribute significantly to the water balance of cerrado ecosystems, and that the hydrological cycle of this biome could change as woody vegetation is replaced by exotic grasses and agricultural crops.

Key-words: evapotranspiration, plant-available water, time-domain reflectometry, TDR

Functional Ecology (2005) **19**, 574–581 doi: 10.1111/j.1365-2435.2005.01003.x

Introduction

For a long time studies on soil-water dynamics and investigations of root systems in ecosystems have mostly been restricted to measurements from the first 0.5 m of soil. However, deep soil explored by deep-rooted plants is now recognized as a major ecosystem compartment with important functional implications (Nepstad *et al.*

†Author to whom correspondence should be addressed. E-mail: rafaelso@yahoo.com

Current address: Department of Integrative Biology, University of California, Berkeley, CA 74000, USA.

1994; Jackson *et al.* 2000). Deep rooting is especially important in seasonally dry environments, such as neotropical savannas, because it enables plants to access water stored deeply in the soil during periods of low water availability and high evaporative demand, and allow them to maintain transpiration and carbon fixation (Sarmiento, Goldstein & Meinzer 1985; Meinzer *et al.* 1999). Canadell *et al.* (1996) have pointed out that tropical savannas are the biome with the deepest mean rooting depth $(15 \pm 5.4 \text{ m})$ and also have the deepest recorded rooting depth (68 m). Although the deep rooting habit of some cerrado plants has been recognized (Rawitscher 1943, 1948; Jackson *et al.* 1999; Franco 2002;

© 2005 British Ecological Society **575** Deep root function in soil water dynamics Oliveira 2004), little is known about their functional significance and contribution to water acquisition. In more mesic ecosystems such as the Amazon rainforest, water stored in deep soil is crucial in maintaining physiologically active canopies during dry periods (Nepstad *et al.* 1994; Hodnett *et al.* 1995; Jipp *et al.* 1998).

Cerrado is the second most extensive biome in Latin America, covering originally an area of almost 2×10^6 km². Land-use change has been occurring rapidly over the past four decades as a result of the increasing demand for cash crops and cattle ranching (Klink & Moreira 2002). The cerrado area is becoming Brazil's most important grain belt and is facing deforestation rates much higher than in the Amazon rainforest (Mueller 2003, Bickel 2004). According to Machado et al. (2004), around 55% of cerrado core has already been cleared or transformed for human uses. The substitution of a complex wood/grass ecosystem for a shallow-rooted grass monoculture is likely to change the hydrological cycle (Klink & Moreira 2002). These changes in land use may ultimately influence local climate (Hoffmann & Jackson 2000). Another major threat to the remaining areas of cerrado is the decrease of the woody component due to the increase of anthropogenic fire frequency, converting the vegetation to a more open and shallow-rooted ecosystem.

The purpose of this study was to: (1) determine seasonal patterns of soil water availability at different soil depths in savanna ecosystems with contrasting tree densities; (2) determine the magnitude and seasonal dynamics of water flux to the atmosphere (evapotranspiration, ET) in each community; (3) investigate the role of deep root systems in the water balance of cerrado ecosystems. The hypotheses we tested were: (1) the treedominated ecosystem (*cerrado denso*) uses more water than the grass-dominated (*campo sujo*); (2) water derived from deep soil (below 1 m) is an important source of water for both vegetation types during the dry season.

Methods

STUDY SITE

The study was carried out between 1996 and 1998 at the Reserva Ecologica do Instituto Brasileiro de Geografia e Estatistica (RECOR-IBGE) Ecological Reserve, 35 km south of Brasília (15°56' S, 47°53' W, altitude 1100 m), in central Brazil. Two adjacent ecosystems (<1 km apart) were selected on the basis of contrasting density of woody plants and similarities of soil type. Cerrado denso is a semi-closed canopy vegetation type with tree cover of $\approx 70\%$, and tree height from 5 to 9 m. Campo sujo is a grassy vegetation with interspersed small shrubs (maximum height ≈ 2.5 m). Woody plant density (>4 cm d.b.h.) in *cerrado denso* is \approx 3350 individuals ha⁻¹ and 960 individuals ha-1 for campo sujo (Ribeiro & Walter 1998). Both areas have been protected against fire for 27 years. The soil type of both physiognomies is clayey red latossol (Oxisol) with high clay content. Surface

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581
 Table 1. Soil bulk density at different soil depths at campo sujo and cerrado denso

| Soil depth (cm) | Soil bulk density (g cm ⁻³)† | | |
|-----------------|--|-----------------|--|
| | Cerrado denso | Campo sujo | |
| 5 | 0.73 ± 0.03 | 0.76 ± 0.02 | |
| 50 | 0.71 ± 0.01 | 0.77 ± 0.02 | |
| 100 | 0.72 ± 0.03 | 0.77 ± 0.03 | |
| 200 | 0.77 ± 0.02 | 0.78 ± 0.02 | |
| 300 | 0.82 ± 0.03 | 0.8 ± 0.03 | |
| 400 | 0.89 ± 0.02 | 0.91 ± 0.06 | |
| 500 | 0.86 ± 0.05 | | |
| 600 | 0.84 ± 0.04 | | |
| 700 | 0.91 ± 0.02 | | |

†Average ± standard error.



Fig. 1. Total monthly rainfall for the period October 1996– October 1998 (source: IBGE/DIEAC-DF).

runoff is not common in the area due to high soil infiltration rates and the flat topography. Soil bulk densities were obtained for both ecosystems at different soil depths and are presented in Table 1.

Rainfall data were collected daily at a weather station 2 km south of the experimental sites. Mean annual rainfall is \approx 1500 mm but is highly variable, with a distinct dry period from May to September (Fig. 1). Rainwater supply was high during the wet season (October–April) of 1997 (17% higher than the long-term average) but low during 1998 (17% lower than average). The dry season of 1998 was the most severe of the 20-year period. Total rainfall for the 1998 dry season was 90% below the average for this period.

EXPERIMENTAL DESIGN AND MEASUREMENT OF SOIL MOISTURE

In each ecosystem, three shafts $(1 \times 2 \times 4 - 8 \text{ m})$ were dug and reinforced with wooden scaffolding to allow us to gain access to deep soil. Volumetric water content (VWC) was measured biweekly using time-domain reflectometry (TDR) from 1996–98 at *cerrado denso*, and from 1997– 98 at *campo sujo*. The TDR wave guides were inserted vertically at the surface (0-0.30 cm) and horizontally at depth by augering 1.5 m into the shaft walls at 0.5, 1 m and at 1 m intervals to 7.5 m depth in *cerrado denso*, and 4 m depth in *campo sujo* (where a plinthite layer was reached and manual excavations were impossible); n = 6sensors per depth per ecosystem. A cable tester (Tektronix model 1502b, Beaverton, Oregon, USA) linked to a laptop computer was used to collect TDR data, as described by Jipp *et al.* (1998).

The TDR technique relates the apparent dielectric constant of the soil (k_a) to VWC (Topp *et al.* 1980). As several studies have considered that the universal k_a (VWC) relationship is inadequate for some soil types (Ponizovsky, Chudinova & Pachepsky 1999; Yu, Warrick & Conklin 1999; Jacobsen & Schjønning 1995), specific calibration for clayey red latossol was carried out using gravimetric sampling near the TDR probes. The VWC of each TDR probe was compared with that determined gravimetrically; 165 soil cores were collected from all depths where a TDR probe was installed in both sites. Soil samples were taken at same level of each TDR probe. In order to determine the VWC of these soil samples, bulk density values obtained from measurements of volume and dry weight of intact soil samples were used. The calibration function was calculated by non-linear regression. Soil samples were obtained on four different dates between May and September 2000.

Water-retention curves were generated using the centrifugation method (Silva & Azevedo 2002). Four intact soil cores were collected from the shaft walls at 30 and 400 cm deep in each ecosystem. The soil samples were submitted to centrifugation for 120 min with rotor speeds equivalent to 6·6, 10·1, 33·4, 101 and 1520 kPa. After each centrifugation the samples were weighed to determine the water content, and after the last centrifugation they were oven-dried for 48 h at 105 °C and the dry weight was determined. The data were generated at the EMBRAPA-Cerrados soil laboratory, and used to estimate soil matric potential. The curves were generated following the van Genutchen (1980) model.

$$\frac{\theta - \theta_r}{\theta_s - \theta_r} = \left[\frac{1}{1 + (\alpha h)^n}\right]^{\left[1 - \frac{1}{n}\right]}$$
(eqn 1)

where θ = soil water content (cm³ cm⁻³); θ_r = residual soil water content (cm³ cm⁻³); θ_s = saturated soil water content (cm³ cm⁻³); *h* = soil water tension generated by centrifugation (kPa); α and *n* = empirical adjustment parameters (kPa⁻¹ and no units).

The parameters α , *n* and θ_r were adjusted by nonlinear regression (EXCEL 2000) and θ_s was used as 88% of total porosity (Haverkami & Parlange 1986).

Plant-available water (PAW) in each layer was calculated as soil water content measured on a given day (VWC_{meas}) minus water content at wilting point. We defined wilting point as the mean of the lowest recorded value of each TDR wave guide over the entire period of study (1996– 98) to obtain a minimum VWC by depth (VWC_{min}):

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581

$$PAW = VWC_{meas} - VWC_{min} \qquad (eqn \ 2)$$

The use of the lowest VWC by depth is an attempt to use a more realistic lower limit of water extraction for drought-adapted plant communities that can draw soil moisture to soil water potentials below the -1.5 MPa threshold commonly used in PAW calculations for annual crops (Bréda et al. 1995; Jipp et al. 1998; Marin, Bouten & Dekker 2000). We have found, with the exception of the upper layers, that the lowest recorded VWC was usually similar to that corresponding to -1.5 MPa (estimated from water retention curves). The minimum water contents for the upper soil layers (30 and 50 cm) corresponded to matric potential values of -5 and -3 MPa. VWC_{min} for all soil depths are presented in Fig. 3. PAW for each soil layer represents an integration of PAW values from several soil depths. For example, for the 0-1 m soil layer we integrated water content data from 30, 50 and 100 cm. PAW can be converted to VWC by the following equation:

$$VWC = (PAW/depth) + VWC_{min}$$
 (eqn 3)

where depth represents the thickness of the soil layer associated with the PAW value $(0-1, 1-4, 4-7\cdot5)$ expressed in mm. For this calculation, VWC_{min} needs to be averaged across the depth increment of interest $(0-1, 1-4, 4-7\cdot5)$. The resulting VWC will be an average value for the depth increment of interest.

Total PAW (PAW_t) was defined as volumetric water content at 0.01 MPa minus water content at wilting point (Reichardt 1988; see area A in Fig. 3). PAW_t was calculated by integrating across the PAW_t values estimated for each sample depth to 7.5 m (*cerrado denso*) and 4 m depth (*campo sujo*).

EVAPOTRANSPIRATION ESTIMATED ON A 15-DAY BASIS BY A SIMPLIFIED WATER-BALANCE EQUATION

$$ET = \Delta VWC + P - D \qquad (eqn 4)$$

where ΔVWC is the change in volumetric water content in the soil profile between successive field measurements; *P* is precipitation; and *D* is drainage out of the measured profile over the same period. As *D* was not measured, all the months when *D* may have been significant were excluded. Therefore ET was calculated only during the dry season and the first half of the wet season (a period when *D* was assumed to be negligible), until the wetting front reached the deepest soil layers.

Soil sampling for fine root estimates (diameter <2 mm) was performed during August 2001 (dry season). Ten sampling points along a 50 m transect in each vegetation type were determined, and at each point the soil sample was collected using an auger (with a cylindrical head of 10 cm diameter and 10 cm deep) at the following depths: 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 100-110, 150-160, 200-210, 250-260 and 300-310 cm. Only roots from the middle section (6 cm) of the soil in the auger were collected to minimize contamination at





Fig. 2. Fine root density distribution to 3 m depth for *campo sujo* and *cerrado denso*. Mean \pm standard deviation, n = 10.

roots from other soil depths. Below 310 cm we collected six soil samples (1 kg each) from shaft walls at each depth where a TDR probe was installed. Roots were separated from soil by a combination of sieving of the soil in suspension through 2, 1 and 0.5 mm nylon mesh, and visual inspection of the soil slurry following sieving (Böhm 1979). Roots were then oven-dried at 60 °C to a constant mass. Root biomasses were converted to root densities per cm³ soil (Fig. 2).

STATISTICAL ANALYSIS

Data were analysed using SYSTAT for Windows 10.2. A two-way ANOVA was performed to verify the effect of depth, ecosystem type and the interaction of both factors over fine root density. Root density data were log-transformed before the analysis. A two-way ANOVA was also performed to verify the effect of ecosystem type and season on deep stocks of PAW.

Results

FINE ROOT BIOMASS

Most of the fine root biomass (92% of the total in both ecosystems) was found in the first metre of soil (Fig. 2). For the first 3 m of soil, fine root biomass distribution was similar in both ecosystems (F = 0.546, P = 0.856). Differences in root density were not significant between the two ecosystems. Fine root density is patchy at depth (Carvalheiro & Nepstad 1996), and the 10 samples used to estimate these densities might have been insufficient to capture differences between ecosystems.

Fine roots were present in all depths sampled. We do not know the maximum rooting depth in either community, but there are reports that roots can extend to at least 18 m in cerrado vegetation (Rawitscher 1948).

TDR CALIBRATION

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581

The following k_a (VWC) relationship ($R^2 = 0.79$) was derived by non-linear regression, using data from both ecosystems:



Fig. 3. Maximum (closed symbols) and minimum (open symbols) volumetric water content registered at each depth from both sites during the dry (May–September) and wet season (October–April). Area A represents total plant available water (PAW_i): water content of soil at 0.01 MPa minus water content at wilting point integrated across all soil depths.



Fig. 4. Water-retention curves for clayed red latossol soils (Oxisol) under *campo sujo* and *cerrado denso*. Data presented are for two depths (30 and 400 cm); points are mean (n = 2); bars are high and low values. The van Genutchen (1980) model was used to generate curves.

VWC =
$$9.56 \times 10^{-2} + 1.21 \times 10^{-2} k_a$$

+ $0.46 \times 10^{-3} k_a^2 - 2.12 \times 10^{-5} k_a^3$ (eqn 5)

SOIL MOISTURE PATTERNS

The minimum recorded VWC was $0.14 \text{ cm}^3 \text{ cm}^{-3}$ at the end of the dry season in the soil surface of *campo sujo*, and $0.16 \text{ cm}^3 \text{ cm}^{-3}$ in *cerrado denso* (Fig. 3). According to our retention curve (Fig. 4) these values correspond to water potentials that can be much more negative than the -1.5 MPa which can be explained by evaporation directly from the soil surface (Franco & Nobel 1990). Other investigators using psychometers measured soil water potentials as low as -5.0 MPa at the peak of the dry season in this community (Franco 2002). Low VWC of $0.16 \text{ cm}^3 \text{ cm}^{-3}$ were also recorded at 50 and 100 cm. However, below 100 cm all minimum VWC recorded corresponded to water potentials above -1.5 MPa.

Seasonal variations of water (PAW) in the 0-1 m soil layer were slightly less under *campo sujo* than in



Fig. 5. Plant-available water in *cerrado denso* (\blacksquare) and *campo sujo* (\square) soils between (a) 0–100; (b) 100–400; (c) 400–750 cm depth. Average \pm SE, n = 6.

cerrado denso, and coupled with rainfall (Fig. 5a). The peaks usually occurred after major rainfall events, and lowest VWC values were usually recorded at the end of dry season (September). Some low values were also recorded during wet months as a result of a drought in the middle of this period (November 1997). Water content at depth was greater in *campo sujo* than in *cerrado denso* in both seasons (P < 0.01; Fig. 5b), and lagged slightly behind rainfall. Recharge of this deep horizon in *campo sujo* usually occurred during the middle of the rainy season (≈ 100 days for the water front to reach the deepest soil layer).

In both ecosystems, the water content of deeper soil layers (1-4 m in campo sujo; 1-7.5 m in cerrado denso) decreased progressively after the onset of the dry season (Fig. 5b,c). Here, two sets of comparisons are offered to quantify the relative contribution of deep roots to total water uptake for both ecosystems. Because we cannot exclude the presence of roots below the plinthite layer at 4 m depth in *campo sujo*, both calculations are

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581 provided as an attempt to bound possible differences between the two ecosystems.

In the first comparison, the maximum soil depth for water extraction in both sites was assumed as 4 m. During the dry season of 1998, PAW from 1 to 4 m declined by 155 mm in campo sujo and 183 mm in cerrado denso (Fig. 5b). For the same period, the decline in PAW for the 0-1 m soil layer was 68 mm for *campo* sujo and 63 mm for cerrado denso (Fig. 5a). Based on this set of comparisons, the water stored in deep soil layers (1–4 m) provided $\approx 70\%$ of the total water used for campo sujo and 75% for cerrado denso. If data for the entire 7.5 m profile for the *cerrado denso* are used, and it is assumed that the campo sujo rooting depth was limited by the plinthite layer at 4 m, more deep water uptake in cerrado denso is calculated. PAW declined 289 mm during the dry season in the 1-7.5 m layer of cerrado denso. This corresponds to 82% of the total water used during this season, and to 134 mm more water extracted from the soil profile than in *campo sujo*.

If fully recharged, the entire soil profile (0-7.5 m) of *cerrado denso* would have 912 mm PAW, whereas *campo sujo* (0-4 m soil profile) would have 486 mm PAW. At *cerrado denso*, PAW reached a maximum of 689 mm (76% of full recharge) in January of 1997 and was reduced to a minimum of 293 mm (25%) at the end of the dry season of 1996. PAW in *campo sujo* reached a maximum of 362 mm (76% of full recharge) in March 1998, while the minimum PAW observed at this site was 155 mm (32% of full recharge) in September 1998. Although *cerrado denso* has a more closed tree canopy that potentially intercepts more rainwater than *campo sujo*, major differences in soil profile recharges between the two ecosystems were not observed.

The relative contribution of shallow vs deep soil compartments was observed for *cerrado denso* during the dry season of 1998, when rainfall input was close to 0 mm. During this period the vertical movement of water was assumed to be minimal because none of the layers had reached field capacity. Water stored at the 0–1 m soil layer contributed 17% to total water used; 1–4 m, 52%; and 4–7.5 m, 31%. Therefore the major source of water for most of the vegetation during this period was from <1 m depth, which agrees with a stable isotope study that investigated the water source of 10 common woody species in the cerrado (Jackson *et al.* 1999). However, vertical unsaturated water fluxes may account for some of the apparent water uptake.

The deepest soil compartment studied in *cerrado denso* (4–7·5 m depth) was recharged during mid-January 1997, when rainfall was above average, and PAW at this soil layer declined steeply only after the onset of the dry season. In the wet season of 1998, however, the water content of the bottom soil compartment was strongly reduced, especially between January and February, when a 52 mm decrease in PAW was observed. This was the greatest drop in PAW between two subsequent months at this layer during the study. During this period, the deeper soil compartment appeared to be a



Fig. 6. Estimated biweekly evapotranspiration (ET) for *cerrado* denso (closed bars) for Δ VWC up to 750 cm depth and estimated ET for *campo sujo* (open bars) for Δ VWC up to 400 cm depth. Estimates are for periods when soil water measured at the beginning and end of the period was less than field capacity, so that drainage could be assumed to be insignificant. Bars represent average daily ET over 15 days.

 Table 2. Estimated evapotranspiration (ET) in campo sujo

 and cerrado denso over the study period

| Vegetation cover | Year | Depth (cm) | ET (mm day ⁻¹)† | |
|------------------|--|------------------------------------|--|---|
| | | | Dry season | Wet season |
| Cerrado denso | 1996–97 1997–98 1996–97 1997–98 | $0-400 \\ 0-400 \\ 0-750 \\ 0-750$ | $0.8 \pm 0.0 \\ 1.8 \pm 0.7 \\ 1.5 \pm 0.0 \\ 2.2 \pm 0.6$ | $\begin{array}{c} 3 \cdot 3 \pm 0 \cdot 6 \\ 3 \cdot 9 \pm 0 \cdot 5 \\ 3 \cdot 7 \pm 0 \cdot 6 \\ 4 \cdot 6 \pm 0 \cdot 7 \end{array}$ |
| Campo sujo | 1997–98 | 0 - 400 | $1 \cdot 3 \pm 0 \cdot 1$ | 3.8 ± 0.4 |

†Average ± standard error.

major supply zone, despite containing smaller root densities than the upper compartment. Rainfall during the first half of this wet season was only 500 mm (42% below average) and was not enough to recharge the upper compartments of the soil. Therefore deep roots appear to be exceptionally important in providing water for vegetation, not only during the dry season but also during periods of high demand for water (early wet season–growing season) associated with below-average rainfall in the middle of the wet season.

EVAPOTRANSPIRATION

Evapotranspiration rates estimated by a simplified waterbalance equation were highest during the wet season and declined during the dry season in both ecosystems (Fig. 6; Table 2). The estimates of ET for *campo sujo* are based on the assumption that water extraction took place from 0 to 4 m soil depth. However, for comparison purposes ET for *cerrado denso* was estimated using the variation in water content for the 0–400 cm soil profile (ET_{0–400}), and then for the entire profile studied (0–750 cm). In both estimates *cerrado denso* had higher ET rates than *campo sujo* during the dry season. Based on the same ET_{0–400} estimates, no difference was found

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581 in ET rates between ecosystems during the wet season. Mean ET rates for *cerrado denso* based on the 0–400 cm profile ranged from 1·8 mm day⁻¹ for dry-season months (June–September 1997) to 3·8 mm day⁻¹ for the early wet-season period (October–January 1998). Mean estimated values of ET based on the entire soil profile for *cerrado denso* (ET_{0–750}) were higher than *campo sujo* during both seasons, ranging from 2·2 mm day⁻¹ for dry-season months to 4·6 mm day⁻¹ for the early wet season (Fig. 6; Table 2). ET in *campo sujo* ranged from a dry-season low of 1·3 to 3·8 mm day⁻¹ in the early wet season (Table 2). ET rates declined 73% in *campo sujo* between wet and dry seasons, and 52% in *cerrado denso*.

Discussion

This study provides evidence that deep water use is important in the water balance of cerrado communities. During the dry season, the deep soil compartment can contribute to as much as 83% of the total water used in a tree-dominated cerrado community. Not only during the dry season, but also in periods of high demand (early wet season–growing season) when there is below average rainfall, deep roots appear to play an exceptionally important role in providing water for vegetation. The pattern of deep soil water exploitation described here for cerrado ecosystems is similar to that observed for eastern Amazonian forests, where water stored deep in the soil corresponded to >75% of the water extracted from the soil (Nepstad *et al.* 1994; Jipp *et al.* 1998).

The ecosystems studied here have contrasting densities of woody species and exhibited different patterns of soil-water extraction that were reflected in different evapotranspiration rates. Our results are consistent with patterns of water use documented in the Amazon Basin, where grass-dominated vegetation (cattle pastures) withdrew a larger portion of its transpirational water demand from surface soil than closed-canopy forests, and where greater dry-season reductions in pasture leaf area index (LAI) were associated with lower dry-season evapotranspiration than the forest (Nepstad et al. 1994; Jipp et al. 1998). In contrast to Amazonian pasture, fine root density in the grass-dominated campo sujo community was not significantly different from cerrado denso throughout the upper 3 m of soil. A comparison of fine roots between cerrado denso and campo sujo ecosystems may require a larger sampling effort because of the heterogeneity of fine root distribution, particularly at depth (Carvalheiro & Nepstad 1996). Moreover, we did not measure the dynamics of root production and mortality, which could be more relevant to correlate with dynamics of soil-water uptake at different depths.

Estimates of total below-ground biomass (TBGB) of roots 1–30 mm in diameter by Castro & Kauffman (1998), from a cerrado study site at the RECOR-IBGE Reserve, suggest that *cerrado denso* has more roots at deeper soil depths than *campo sujo*. More than 80% of TBGB occurred in the upper 30 cm of the soil in *campo sujo*, while in *cerrado denso* 71% of TBGB occurred at

this soil depth, suggesting that a greater proportion of tree roots were present at deeper levels in *cerrado denso* (Castro & Kauffman 1998). Most of the root biomass in our study was also near the surface in both ecosystems, yet the modest root biomass below 1 m was important for water uptake (Figs 2 and 5).

Assuming that water uptake is negligible from below the plinthite layer in the *campo sujo* site, the *cerrado* denso ecosystem - a plant community with greater tree density - used more soil water than *campo sujo*, even when only the uptake from 0-4 m depth was considered. Campo sujo is dominated by shallow-rooted grasses that have above-ground biomass production coupled with the drying and rewetting cycles of upper soil horizons, and leaves that senesce immediately at the end of the wet season (Silva & Klink 2001). Silva & Klink (2001) estimated a reduction in LAI of $\approx 50\%$ during the dry season for the grass component of an adjacent area. Therefore smaller water content in the upper soil of campo sujo, lower total water use, and a sharper decrease in ET during the dry season than cerrado denso are consistent with the rooting pattern and phenological dynamics of the grass component in this community. Differences in canopy interception and subsequent evaporation may also account for a large amount of the difference between dry- and wet-season ET values (Seyffarth 1995).

Campo sujo ET values reported here also lie within the range of values reported by Dunin et al. (1997); Santos (1999); Quesada et al. (2004) for adjacent campo sujo areas. Based on TDR measurements down to 1.5 m depth, Dunin et al. (1997) estimated an average ET rate of 2.8 mm day^{-1} during the early wet season of 1996. ET rates calculated for an adjacent area in 2000 by Quesada et al. (2004), using a water balance based on neutron-probe measurements, ranged from 1.6 to 2.8 mm day⁻¹. Using an energy balance approach, Santos (1999) estimated ET rates ranging from 1.4 mm day^{-1} at the end of the dry season to 2.8 mm day¹ in the early wet season. Our early wet season ET estimate for campo sujo (October 1997) is 3.0 mm day^{-1} . Therefore the similarity of campo sujo ET estimates derived from different methodologies supports our assumption that there was no substantial water uptake from <4 m during the early wet season.

Higher rates of dry-season ET, and perhaps also higher wet-season ET in *cerrado denso*, can be explained largely by the greater density of the woody component, predominantly deep rooted, that can exploit water stored at deeper soil compartments. Our estimates of ET are in good agreement with eddy correlation estimates shown by Maitelli & Miranda (1991); Miranda & Miranda (1992); Miranda *et al.* (1997) in a nearby cerrado site of similar structure. In these studies, ET estimates ranged from 1·9 mm day⁻¹ during the dry season to 3·5 mm day⁻¹ in the wet season. The pronounced seasonal differences in total ET may be caused more by dry-season reductions in leaf area than by dry-season increases in leaf resistance to vapour flux. Pinto (1998)

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581 followed the phenological dynamics of seven woody species at our study site, and estimated a decrease of 30% in LAI after the onset of the dry season. Meinzer *et al.* (1999) studied the seasonal regulation of transpiration of four evergreen woody species in a cerrado site and found that only one species showed a greater daily water use in the wet season. Their results suggest that transpiration in these species is limited in both seasons by strong stomatal control, probably influenced by high atmospheric demand and hydraulic constraints arising from their deep rooting depth.

In this study we provide evidence that two ecosystems with contrasting tree densities have different patterns of soil water use. Based on these results, we can speculate about how human-induced changes in woody density will affect the water balance of these ecosystems. Large expanses of natural cerrado vegetation have been transformed from a mixture of trees and grasses into planted pastures and crops. Agricultural expansion has also led to an increase in burning, and areas still covered with natural vegetation are now burned almost every year (Klink & Moreira 2002). Fire tends to favour herbaceous plants at the expense of woody plants, especially as it has a negative effect on the establishment of tree and shrub seedlings (Hoffmann 1996). Therefore in the future grass-dominated ecosystems could occupy most of the cerrado area. Based on our results, we expect that the current shift toward grass-dominated ecosystems in the Brazilian savannas will increase deep soil water storage and reduce ET because of less water uptake by deep roots, especially during the dry season. Assuming that local precipitation is at least partially dependent on regional rates of evapotranspiration, the cerrado climate could become drier (Hoffmann & Jackson 2000). Model simulations of the effects on regional climate of the conversion of natural cerrado into open grasslands have shown precipitation reduced by $\approx 10\%$, an increase in the frequency of dry periods within the wet season, changes in albedo, and mean surface air temperature increased by 0.5 °C (Hoffmann & Jackson 2000).

Acknowledgements

This study was supported by grants from NSF, A.W. Mellon Foundation, CNPq, CAPES, FAP-DF, IAI-CRN 040, LBA/NASA, and RECOR-IBGE site 3 of PELD/CNPq. We would like to thank Dr Heloisa Miranda and Dr Mercedes Bustamante for their helpful comments on the manuscript. We are also very grateful for the field and logistic assistance provided by EMBRAPA-Cerrados, Beth Belk, Paul Lebfreve, Karen Schwalbe, João B. Souza, Tucura, Bate, Adilson Coelho, Manuel Nascimento, José Gervásio and Tiago.

References

Bickel, U. (2004) Brasil: expansão da soja, conflitos sócioecológicos e segurança alimentar. MSc thesis, School of Agronomy, University of Bonn, Germany. Deep root function in soil water dynamics

- Böhm, W. (1979) *Methods of Studying Root Systems* (eds W.D. Billings, D.F. Golley, A.O.L. Lange, *et al.*). Ecological Studies No. 33, Springer-Verlag, Berlin.
- Bréda, N., Granier, A., Barataud, F. et al. (1995) Soil water dynamics in an oak stand. Plant and Soil 172, 17–27.
- Canadell, J., Jackson, R.B., Ehleringer, J.R. *et al.* (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**, 583–595.
- Carvalheiro, K.D. & Nepstad, D.C. (1996) Deep soil heterogeneity and fine root distribution in forests and pastures of eastern Amazonia. *Plant and Soil* 182, 279–285.
- Castro, E.L. & Kauffman, J.B. (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical Ecology* 14, 263–283.
- Dunin, F.X., Miranda, H.S., Miranda, A.C. et al. (1997) Evapotranspiration responses to burning of Campo Sujo Savanna in Central Brazil. Proceedings of the Bushfire '97 Conference (eds B.J. Mckaige, R.J. Williams & W.M. Waggitt), pp. 146–151. CSIRO, Winnellie, Australia.
- Franco, A.C. (2002) Ecophysiology of woody plants. *The Cerrados of Brazil* (eds P.S. Oliveira & R.J. Marquis), pp. 178–197. Columbia University Press, New York, USA.
- Franco, A.C. & Nobel, P.S. (1990) Influences of root distribution and growth on predicted water uptake and interspecific competition. *Oecologia* 82, 151–157.
- van Genutchen, M.T. (1980) A closed-form equation for predicting the hydraulic properties of unsaturated soils. *Soil Science Society of America Journal* 44, 892–898.
- Haverkami, R. & Parlange, J.Y. (1986) Predicting the water retention curve from particle-size distribution: 1. sandy soils without organic matter. *Soil Science* **142**, 325–339.
- Hodnett, M.G., Silva, L.P., Rocha, H.R. *et al.* (1995) Seasonal soil water storage changes beneath central Amazonian rainforest and pasture. *Journal of Hydrology* 170, 233–254.
- Hoffmann, W.A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology* 84, 383–393.
- Hoffmann, W.A. & Jackson, R.B. (2000) Vegetation–climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate* **39**, 145–176.
- Jackson, P.C., Meinzer, F.C., Bustamante, M. *et al.* (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology* **19**, 717–724.
- Jackson, R.B., Schenk, H., Jobbágy, E. *et al.* (2000) Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* 10, 470–483.
- Jacobsen, O.H. & Schjønning, P. (1995) Comparison of TDR calibration functions for soil water determination. *Proceedings* of the Symposium: Time-Domain Reflectometry Applications in Soil Science (eds L.W. Petersen & O.H. Jacobsen), pp. 25–33. Danish Institute of Plant and Soil Science, Lyngby, Denmark.
- Jipp, P.H., Nepstad, D.C., Cassel, D.K. et al. (1998) Deep soil moisture storage and transpiration in forest and pastures of seasonally dry Amazonia. *Climate Change* 39, 395–412.
- Klink, C.A. & Moreira, A.G. (2002) Past and current human occupation, and land-use. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (eds P.S. Oliveira & R.J. Marquis), pp. 69–88. Columbia University Press, New York, USA.
- Machado, R.B., Ramos Neto, M.B., Pereira, P. et al. (2004) Estimativas de Perda da Área do Cerrado Brasileiro. Conservation International do Brasil, Brasília.
- Maitelli, G.T. & Miranda, A.C. (1991) Evapotranspiração e fluxos de energia no Cerrado – Estação Chuvosa. Anais da Academia Brasileira de Ciências 63, 265–272.

© 2005 British Ecological Society, *Functional Ecology*, **19**, 574–581

Marin, C.T., Bouten, I.W. & Dekker, S. (2000) Forest floor water dynamics and root water uptake in four forest ecosystems in northwest Amazonia. *Journal of Hydrology* 237, 169–183.

- Meinzer, F.C., Goldstein, G., Franco, A.C. *et al.* (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. *Functional Ecology* 13, 273–282.
- Miranda, A.C. & Miranda, H.S. (1992) Impactos de processos ecológicos: estresse hídrico. Alternativas de Desenvolvimento dos Cerrados: Manejo e Conservação dos Recursos Naturais Renováveis (ed. B.F.S. Dias), pp. 30–34. FUNATURA, Brasília.
- Miranda, A.C., Miranda, H.S., Lloyd, J. *et al.* (1997) Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. *Plant, Cell & Environment* 20, 315–328.
- Mueller, C. (2003) Expansion and Modernization of Agriculture in the Cerrado – the Case of Soybeans in Brazil's Center-West. Working Paper 306. Department of Economics, University of Brasilia, Brasilia.
- Nepstad, D.C., Carvalho, C.R., Davidson, E.A. *et al.* (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**, 666–669.
- Oliveira, R.S. (2004) Comparative water use and water acquisition strategies of trees from the Brazilian Cerrado and Amazônia. PhD thesis, University of California, Berkeley, CA, USA.
- Pinto, A.S. (1998) A relação entre fenologia de espécies lenhosas e a disponibilidade hídrica no Cerrado. MSc thesis, University of Brasilia, Brasília.
- Ponizovsky, A.A., Chudinova, S.M. & Pachepsky, Y.A. (1999) Performance of TDR calibration models as affected by soil texture. *Journal of Hydrology* 218, 35–43.
- Quesada, C.A., Miranda, A.C., Hodnett, M.G. et al. (2004) Seasonal and depth variation of soil moisture in a burned open savanna (*campo sujo*) in central Brazil. *Ecological Applications* 14(suppl.), 33–41.
- Rawitscher, F. (1943) Profundidade dos solos e vegetação em campos cerrados do Brasil Meridional. Anais da Academia Brasileira de Ciências 15, 267–296.
- Rawitscher, F. (1948) The water economy of the vegetation of the campos cerrados in Southern Brazil. *Journal of Ecology* 36, 237–268.
- Reichardt, K. (1988) Capacidade de compo. Revista Brasileira de Ciências do solo 12, 211–216.
- Ribeiro, J.F. & Walter, B.M.T. (1998) Fitofisionomias do Bioma Cerrado. *Cerrado: Ambiente e Flora* (eds M.S. Sano & S.P. Almeida), pp. 89–152. EMBRAPA/CPAC, Planaltina, Brazil.
- Santos, A.J.B. (1999) Fluxos de Energia, Carbono e Água em Vegetação de Campo Sujo. MSc thesis, Universidade de Brasília, Brasília.
- Sarmiento, G., Goldstein, G. & Meinzer, R. (1985) Adaptive strategies of woody species in neotropical savannas. *Biological Reviews* 60, 315–355.
- Seyffarth, J.A.S. (1995) Interceptação de chuva em cerrado sensu stricto sob diferentes regimes de queima. MSc. Thesis, Universidade de Brasília, Brasília.
- Silva, E.M. & Azevedo, J.A. (2002) Influência do período de centrifugação na curva de retenção de água em solo de Cerrado. *Pesquisa Agropecuária Brasileira* 37, 1487–1494.
- Silva, D. & Klink, C.A. (2001) Dinâmica de foliação e perfilhamento de duas gramíneas C₄ e uma C₃ nativas do Cerrado. *Revista Brasileira de Botânica* 24, 441–446.
- Topp, G.C., Davis, J.L. & Annan, A.P. (1980) Electromagnetic determination of soil water content: measurement in coaxial transmission lines. *Water Resources Research* 16, 574–582.
- Yu, C., Warrick. A.W. & Conklin, M.H. (1999) Derived functions of time-domain reflectometry for soil moisture measurement. *Water Resources Research* 35, 1789–1796.

Received 26 August 2004; revised 1 March 2005; accepted 30 March 2005

581