

## Hydraulic lift in a Neotropical savanna: Experimental manipulation and model simulations

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### SUMMARY

The objective of this study was to assess the magnitude of hydraulic lift in Brazilian savannas (Cerrado) and to test the hypothesis that hydraulic lift by herbaceous plants contributes substantially to slowing the decline of water potential and water storage in the upper soil layers during the dry season. To this effect, field observations of soil water content and water potentials, an experimental manipulation, and model simulations, were used. Savannas of central Brazil exhibit consistent changes in tree density along shallow topographic gradients, from open savannas with relatively few trees in the lower portions of the topographic gradients to woodlands with a relatively high density of trees in the upper portions of the gradient. Herbaceous plant abundance follows the opposite trend. The diel recovery of soil water storage was higher in sites with more abundant herbaceous vegetation. Experimental removal of the above ground portion of herbaceous plants in a site with low tree density, during the dry season, substantially enhanced diel recovery of water potentials in the upper soil layers, consistent with the release of hydraulically lifted water from their shallow roots. In a site with high tree density, the release of hydraulically lifted water by woody plants contributed only 2% to the partial daily recovery of soil water storage, whereas the herbaceous layer contributed the remaining 98%. Non saturated water flow in the same savanna type contributed 8% to the partial daily recovery of soil water potential at the beginning of the dry season, decreasing to near 0% after 20 days of drought. During a 70-day rainless period the soil water potential dropped to  $-2.0$  MPa near the soil surface. The simulation model predicted that without hydraulic lift, water potential in the upper soil layers in relatively dense savannas would have dropped to  $-3.8$  MPa. The maximum contribution of hydraulic lift to the upper 100 cm of soil was  $0.7$  mm day<sup>-1</sup> near the middle of the dry season. During the peak of the dry season, hydraulic lift can replace 23% of the ecosystem evapotranspiration in a site with high tree density and consequently greatly influences the water economy and other ecosystem processes in the Cerrado.

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### 1. Introduction

Hydraulic lift, the movement of water via roots from moist, deeper soil layers to relatively dry shallow soil layers, is widespread among Brazilian savanna (Cerrado) tree species as shown by sap flow measurements in roots and stable isotope labeling techniques (e.g. Scholz et al., 2002, 2008; Moreira et al., 2003). Vertical water potential gradients in the soil and plants with shallow and deep roots are a prerequisite for hydraulic lift to occur.

Deciduous and brevideciduous Cerrado trees that have a dimorphic root system with both shallow and tap roots are involved in lifting water from deeper soil layers, whereas evergreen Cerrado trees apparently do not hydraulically lift water (Scholz et al., 2008). Release of hydraulically lifted water into the upper soil layers by Cerrado woody plants contributes only 1% of their total daily water use (Scholz, 2006; Scholz et al., 2008) and about 2% to the partial daily recovery of soil water storage (Scholz, 2006). Even though this process does not contribute substantially to the plant's water economy, it can help to maintain root hydraulic conductivity at a level that prevents complete rectification sensu Nobel and Sanderson (1984) in lateral roots of many Cerrado woody plants exploring dry soil layers (Scholz et al., 2008).

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Previous observations have allowed us to hypothesize that the amount of water released by shallow roots of Cerrado trees is not sufficient to produce the diurnal variations in soil water content and soil water potentials observed in the upper soil horizons (Moreira et al., 2003; Scholz et al., 2008). The only other candidates for generating such large diel oscillations in soil water potential are herbaceous plants (grasses and dicot plants) that have a large abundance of roots in the upper 100 cm of soil (Oliveira et al., 2005) and/or non-saturated water flow. The substantial decrease in the leaf area index of herbaceous species during the dry season makes the aboveground portion of these plants (Hoffmann et al., 2005) a weak competitor for hydraulically lifted water that instead of being lost to the atmosphere by transpiration remains in the upper soil layers. Leffler et al. (2005) demonstrated that roots of grasses from East African savannas can hydraulically lift water from deeper soil layers in the absence of living aboveground tissue. It is not known what the water potentials of upper soil layers would be for *Neotropical savanna* in the absence of hydraulic lift carried out by herbaceous plants.

Tropical savanna is the second most extensive vegetation type in South America, and the Cerrado of central Brazil forms the largest regional system (Goodland, 1971). The principal factors influencing the structure of Cerrado vegetation include not only a pronounced seasonality of precipitation, frequent fires and low soil fertility (Haridasan, 2000), but also high temperatures and low humidity. The low relative humidity in the Cerrado imposes a consistently high evaporative demand during the prolonged dry season that can last 5 months. During this period, low water contents and negative water potentials are observed in the upper soil layers (Quesada et al., 2004, 2008; Bucci et al., 2008; Scholz et al., 2008) and consequently the shallow rooted herbaceous plants undergo a rapid decline in leaf area index (Hoffmann et al., 2005). More abundant water at greater depth is utilized by the deeply rooted trees (Bucci et al., 2008), and could also be used to some extent by herbaceous plants with relatively deep roots. Most trees maintain a relatively large gas exchange surface during the dry season, and even the deciduous trees and most evergreen trees renew their leaf crop before the beginning of the rainy season (Franco et al., 2005; Lenza and Klink, 2006).

The objectives of this study were to assess the magnitude of hydraulic lift in Brazilian savannas differing in the relative abundance of trees and herbaceous plants, and to test the hypothesis that herbaceous plants contribute substantially to the release of hydraulically lifted water into the upper soil layers during the dry season. To this end, field observations of soil water content and water potentials across the soil profile were obtained in five savanna types, and a manipulative experiment as well as model simulations were used. Soil water content was measured with capacitance sensors, and soil water potentials were measured psychrometrically in the upper 100 cm of the soil profile. An experimental manipulation involving the removal of the aboveground part of the herbaceous layer from experimental plots in a savanna with low tree density (campo cerrado) was performed. A model previously developed by Ryel et al. (2002) describing water movement within the soil via both non-saturated flow and hydraulic lift was modified and expanded to include algorithms representing nocturnal transpiration, transpiration from both woody and herbaceous plants, and soil non-homogeneity. The model was validated using predictions of time courses of soil water potential at several depths for a campo cerrado site. Soil properties and leaf area index of trees and herbaceous plants were also studied along the tree density gradient in order to calculate model parameters based on a comprehensive knowledge of soil and vegetation characteristics.

## 2. Materials and methods

### 2.1. Site description and plant material

The present study was carried on at the Instituto Brasileiro de Geografia e Estatística (IBGE) research station located 33 km south of Brasilia (15°56'S, 47°53'W, altitude 1100 m), Brazil. The IBGE reserve contains all of the major physiognomic types of Cerrado vegetation. Cerrado vegetation contains different combinations of savanna types organized spatially along gradients of decreasing abundance of woody plants, from woodland with a closed canopy (cerradão) to campo sujo, an open savanna with scattered trees and shrubs, over distances of only a few km (Table 1). Average annual precipitation is about 1500 mm with a pronounced dry season from May to September. The months of June, July and August are often devoid of precipitation. Mean monthly temperature ranges from 19 to 23 °C, and diurnal temperature fluctuations of 20 °C are common during the dry season. Soil physical properties were analyzed by the soil laboratory of the Agricultural Research Center for the Cerrado region (EMBRAPA, Brazil). Four soil samples per depth (10, 20, 30, 60 and 100 cm) were taken in each savanna type.

### 2.2. Soil water potential and water content

Soil psychrometers (PST-55, Wescor, Logan, UT) were used to continuously monitor soil water potential ( $\Psi_{\text{soil}}$ ) at 0.10, 0.20, 0.30, 0.60 and 1.00 m depths ( $n = 4$  per depth and per savanna type). Before placement in the field, the psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown & Bartos (1982). Soil water potential was measured every 30 min in the psychrometric mode with a 30-s cooling time and recorded with a data logger (CR-7, Campbell Scientific, Logan, UT, USA). Results were corrected for potential temperature gradients between bulk soil and the psychrometers according to Brown and Bartos (1982). An integrated  $\Psi_{\text{soil}}$  for the 20–60 cm layer was estimated by averaging the values for all psychrometers between these depths. Daily partial recovery of  $\Psi_{\text{soil}}$  for the 20–60 cm layer and 20, 30 and 60 cm soil layers was estimated by subtracting diel minimum  $\Psi_{\text{soil}}$  from the subsequent diel maximum values.

Soil volumetric water content was continuously monitored with multi-sensor frequency domain capacitance probes (Paltineanu and Starr, 1997) at three to four replicate locations per site during three to four days each month. The highly sensitive probes contained six annular capacitance sensors (Sentek PTY Ltd., Adelaide, Australia) positioned at depths of 0.20, 0.30, 0.60, 1.00, 1.50 and 2.00 m mounted on a single plastic rail and were placed in weatherproof PVC access tubes. All sensors were monitored every 30 min and the measurements stored by a data logger (Model RT6, Sentek). Each sensor was calibrated in the field for the air and water frequency reading endpoints for determination of the normalized frequency. The factory default calibration equation was used. Soil water storage (measured in mm) was calculated by summing the water content for each 0.10-m sensor. When there was a gap between sensors (e.g. 0.30 or 0.60 m), water storage in the intervening layer was interpolated as an average of the sensors above and below the layer summed over the number of 0.10-m intervals in the layer. Mean daily partial recovery of soil water storage for the 20–60 cm layer was estimated by subtracting diel minimum water storage values from the subsequent diel maximum values.

### 2.3. Leaf area index and tree basal area

Values of ground layer leaf area index (LAI) for graminoids and herbaceous dicots for different Cerrado physiognomies were taken

**Table 1**

Tree density, tree basal area per stand, leaf area index of trees (LAI<sub>tree</sub>) and leaf area index of the ground layer (herbaceous plants and grasses; LAI<sub>herb</sub>) obtained in September of 2003, soil water potential differences between 20 and 100 cm depths ( $\Delta\Psi_{\text{soil}(20-100\text{ cm})}$ ) during August of 2002, and mean soil physical properties at 10 cm and at 100 cm depth (field capacity, bulk density and porosity) in the five Cerrado physiognomies.

	campo sujo	campo cerrado	cerrado sensu stricto	cerrado denso	cerradão
Tree density (ind ha <sup>-1</sup> ) <sup>*</sup>	930	1733	2690	2828	3300
Tree basal area (m <sup>2</sup> ha <sup>-1</sup> ) <sup>*</sup>	4.32	4.39	10.70	18.16	26.63
LAI <sub>tree</sub> <sup>**</sup>	1.5	1.24	1.73	1.67	2.91
LAI <sub>herb</sub> <sup>**</sup>	0.90	1.03	0.55	0.60	0.37
$\Delta\Psi_{\text{soil}(20-100\text{ cm})}$ (MPa) <sup>*</sup>	1.1	1.18	1.13	0.68	0.11
Soil field capacity (%)					
10 cm	45 ± 0.6	45 ± 1.1	45 ± 2.1	48 ± 2	50 ± 1
100 cm	37 ± 1.7	44 ± 0.6	40 ± 0.5	42 ± 1	41 ± 1
Soil density (g cm <sup>-3</sup> )					
10 cm	0.90 ± 0.1	0.85 ± 0.02	0.85 ± 0.02	0.81 ± 0.07	0.85 ± 0.21
100 cm	1.11 ± 0.0	0.97 ± 0.01	1.15 ± 0.02	1.13 ± 0.19	1.06 ± 0.01
Porosity (%)					
10 cm	62 ± 09	65 ± 0.3	64 ± 0.8	68 ± 2	65 ± 0.7
100 cm	55 ± 2.4	63 ± 0.6	56 ± 09	57 ± 8	58 ± 1.4

<sup>\*</sup> Data from Bucci et al. (2008).

<sup>\*\*</sup> Data from Hoffmann et al. (2005).

from Hoffmann et al. (2005). Leaf area index was determined using a LAI 2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA). Measurements were performed in five Cerrado physiognomies with different tree density in September 2003 according to the methodology described by Hoffmann et al. (2005). LAI values of treatment and control plots were estimated by destructive methods.

The total tree basal area per unit of ground (m<sup>-2</sup> ha<sup>-1</sup>) was taken from Bucci et al. (2008). It was estimated in ten 10 m × 20 m plots for all physiognomies with the exception of the cerradão (highest density physiognomy) where only five 10 m × 20 m plots were used. In each plot, all individuals larger than 1-m-tall and more than 4-cm DBH were identified and measured.

#### 2.4. Manipulative experiment

Four 15-m<sup>2</sup> plots in a savanna site with low tree density (campo cerrado) were established for assessing the effects of aboveground herbaceous plants on the magnitude of daily recovery of  $\Psi_{\text{soil}}$ . One screen-cage soil psychrometers, as described above, were placed at 20, 30, 60 and 100 cm soil depth in each plot ( $n = 2$  per depth and treatment) at the end of the dry season. On September 19, 2006, only herbaceous aboveground biomass (grass and dicots) was manually cut from two randomly chosen plots. The biomass removed was returned to the soil surface to avoid an increase in the evaporation rates resulting from exposure of bare soil. Green leaf area index of each plot was determined by destructive harvest of the ground-layer vegetation within two 0.5 m × 0.5 m subplots in the control and treatment plots. In control plots the subplots were located far from the psychrometers and in the treatments plots LAI was obtained when aboveground material was removed. All ground-layer vegetation was harvested from the sub-plots, and the surface area of dicots and grass leaves was determined. Predawn and midday leaf water potentials ( $\Psi_L$ ) were measured with a pressure chamber (PMS, Corvallis, OR).

#### 2.5. Model development

To describe the vertical water movement within the soil during the dry season, a model developed by Ryel et al. (2002) was modified to incorporate algorithms representing nocturnal transpiration, water loss by transpiration from both woody and herbaceous plants, and soil non-homogeneity (soil layers with different physical properties). It was parameterized using physical

properties of the Cerrado soils and information on diurnal and seasonal changes in herbaceous and woody plant transpiration measured in the study sites. The one-dimensional model simulated vertical changes in soil water content as a result of non-saturated water flow, hydraulic lift, and water consumption due to plant transpiration. In the present study, water input by precipitation and surface evaporation was not included in the model algorithms. The soil profile was assumed to consist of 11 layers with water moving between adjacent layers: The first 10 layers were 10 cm thick and the 100–200 cm soil layer was not subdivided. The soil water potential below 200 cm was assumed to be zero during the peak of the dry season, which is consistent with previous observations of soil water content (Bucci et al., 2008).

The changes in soil water content in the  $i$ -soil layer were expressed as:

$$\frac{dQ_i}{dt} = J_i + R_i - T_i \quad (1)$$

where  $Q_i$  (cm) is the amount of water in the  $i$ -layer,  $t$  (h) is the time,  $J_i$  (cm h<sup>-1</sup>) is the non-saturated water flow of the  $i$ -layer;  $R_i$  (cm h<sup>-1</sup>) is the amount of water hydraulically lifted by plant roots to the  $i$ -layer, and  $T_i$  (cm h<sup>-1</sup>) is the amount of water loss by transpiration (water uptake) from the  $i$ -layer.

Field data for model parameterization were collected in a savanna site (cerrado denso) in the IBGE reserve. Parameters used in the model are given in Table 2.

#### 2.6. Non-saturated flow

Following Buckingham–Darcy law (Jury et al., 1991), vertical non-saturated water flow in the soil column was described as:

$$J_i = -K(\theta_i) \left[ \left( \frac{d\Psi_i}{dz} \right) + 1 \right] \quad (2)$$

where  $J_i$  (cm h<sup>-1</sup>) is the net water flow in the  $i$ -layer,  $K(\theta_i)$  (cm h<sup>-1</sup>) is the non-saturated hydraulic conductivity for volumetric water content,  $\theta_i$  (cm<sup>3</sup> cm<sup>-3</sup>) in layer  $i$  and  $d\Psi_i/dz$  is the soil-matric potential gradient (MPa cm<sup>-1</sup> or cm cm<sup>-1</sup>) between the extremes of the soil  $i$ -layers, and  $z$  (cm) is vertical thickness (cm) of the soil. Non-saturated hydraulic conductivity was calculated as:

$$K_i(\theta_i) = K_s S_i^l [1 - (1 - S_i^l/m)^m]^2 \quad (3)$$

where  $l$  is a connectivity parameter between soil pores and assumed to be 0.5 for a wide range of soil types (Mualem, 1976),  $K_s$  is the saturated hydraulic conductivity,  $m$  is a empirical constant depending on soil characteristics, and  $S_i$  is the effective degree of saturation or reduced water content in layer  $i$  ( $0 \leq S_i \leq 0$ ), defined as:

$$S_i = \frac{(\theta_i - \theta_r)}{(\theta_s - \theta_r)} \quad (4)$$

where  $\theta_r$  is residual volumetric water content indicating the maximum soil water amount that does not contribute to the liquid phase, and  $\theta_s$  is volumetric water content in layer  $i$ .

To describe the relationship between volumetric water content and matric potential of layer  $i$  the equation of van Genuchten (1980) was used:

$$\theta_i = \theta_r + \frac{(\theta_s - \theta_r)}{[1 + (\alpha \Psi_i)^m]^n} \quad (5)$$

where  $\alpha$  ( $\text{cm}^{-1}$ ),  $m$  ( $m = 1 - (1/n)$ ) and  $n$  are empirical parameters according to Maulem model, which depends on soil characteristics, and  $\theta_s$  and  $\theta_r$  are saturated and residual volumetric water content, respectively

The van Genuchten (1980) physically based mathematical model was used for determination of non-saturated soil characteristics functions due to its ability to describe well those functions for oxisols, which are the dominant soils in the Cerrado (Tomasella and Hodnett, 1997).

### 2.7. Hydraulic lift

The model describes water hydraulically lifted by roots as a function of the amount of active roots, rhizosphere conductance, and temporal behavior of the process. According to the model, the hydraulic lift stops at dawn and begins in the evening when leaf water demand ceases or decreases. It is assumed that water movement between layers is limited by the layer with lower active root amounts and by the low rhizosphere conductivity in the soil layer where water is released. Therefore net water movement into layer  $i$  from others layers  $j$  was expressed as:

$$R_i = C_{R\max} \sum_{(j>i)} \Delta \Psi_{i,j} \min\{c_i, c_j\} \left[ \frac{(r_i * r_j)}{(1 - r_i)} \right] E_{\text{Night}} \quad (6)$$

where  $C_{R\max}$  ( $\text{cm MPa}^{-1} \text{h}^{-1}$ ) is the maximum soil–root hydraulic conductance of the whole active root system,  $c_i$  is a factor that takes into account the variation in rhizosphere conductance as a function of changes in  $\Psi_i$ ,  $r_i$  is a fraction of active roots in layer  $i$  and  $E_{\text{Night}}$  is a function of “activation” of the hydraulic lift process with values varying between 1 (during nighttime) and 0 (during daytime). Relative soil–root hydraulic conductance was modeled using an empirical relationship (Ryel et al., 2002):

$$c_i = \frac{1}{[1 + (\Psi_i/\Psi_{50})^b]} \quad (7)$$

where  $\Psi_{50}$  (MPa) is the soil water potential at 50% loss of soil–root hydraulic conductance and  $b$  is an empirical constant.

### 2.8. Transpiration

Water loss by transpiration was assumed to be primarily limited by the soil–root conductance ( $c_i$ ) and by the amount of roots in each layer ( $r_i$ ). Contribution of  $i$ -layer to transpiration ( $T_i$ ) was modeled as:

$$T_i = (T_T + T_H) r_i c_i \quad (8)$$

where  $T_T$  represents the maximum whole tree canopy transpiration rate per hour ( $\text{cm h}^{-1}$ ) and  $T_H$  represents the maximum

**Table 2**

Parameter values used in the model.

Parameter	Value
Saturated soil water content ( $\theta_s$ , $\text{cm cm}^{-3}$ )	
- 10 cm	0.80
- 20 cm	0.65
- 30 cm	0.53
- 60 cm	0.47
- 100 cm	0.46
Residual volumetric soil water content ( $\theta_r$ , $\text{cm cm}^{-3}$ )	0.2
Fitting parameter for soil water retention curves ( $\alpha$ , $\text{cm}^{-1}$ )	
- 10 cm	0.2800
- 20 cm	0.1500
- 30 cm	0.1000
- 60 cm	0.0600
- 100 cm	0.0066
Fitting parameter for soil water retention curves ( $n$ )	
- 10 cm	1.20
- 20 cm	1.19
- 30 cm	1.18
- 60 cm	1.16
- 100 cm	1.16
Saturated soil hydraulic conductivity ( $K_s$ , $\text{cm h}^{-1}$ )	
- 10 cm	100.0
- 20 cm	45.5
- 30 cm	4.9
- 60 cm	4.9
- 100 cm	5.8
Root conductivity of water for all roots ( $C_{RT}$ , $\text{cm MPa}^{-1} \text{h}^{-1}$ )	0.129
$\Psi_{\text{soil}}$ where $C_{RT}$ reduced by 50% ( $\Psi_{50}$ , MPa)	-0.80
Parameter ( $b$ )	1.61
Maximum transpiration rate ( $T_{RT, \max}$ , $\text{cm h}^{-1}$ )	0.057
HR activation ( $E_{\text{Night}}$ )	1 or 0

herbaceous and shrub transpiration rate per hour ( $\text{cm h}^{-1}$ ) considering also the nocturnal period.

Maximum stand-level tree transpiration ( $T_T$ ) for a cerrado denso site during the dry season was obtained from Bucci et al. (2008). Ground layer evapotranspiration ( $E_H$ ) was estimated using an open top chamber (OTC) during the dry season. Nine replicates were obtained on grasses and herbaceous dicots at 2-h intervals during the course of a day. Evapotranspiration of the vegetation enclosed by the chamber ( $0.5 \text{ m}^2$ ) was calculated using the difference between water vapor density of air entering and exiting the chamber. The chamber was similar to that described by Hutley et al. (2000). It consisted of a cylindrical base of 0.80 m diameter and 0.95 m height cone made from clear acrylic plastic and a metal frame supporting the clear plastic. The top of the cone had an opening (exit port) of 0.2 m diameter. Total chamber height was 1.66 m and the volume enclosed was  $0.64 \text{ m}^3$ . Air was pumped into the chamber using an inlet fan mounted near its base and the flow rates were measured at the exit port using a propeller anemometer. Water vapor densities of air entering and leaving the chamber were measured with a dew point hygrometer (HR 33T, YES, Yankee environment system, Ontario, Canada). Air streams were ducted to an enclosure containing the dew point hygrometer using Beva-Line tubing at flow rates of  $8 \text{ l min}^{-1}$  and controlled by a mass flow controller. Output from the hygrometer was recorded at 1 s intervals with a datalogger (21X, Campbell Scientific, UT, USA). The air stream to the hygrometer was switched between inflow and outflow every 2 min. Air temperature of the out-going air stream was between 1 and 2 °C above ambient. Evapotranspiration was calculated as:

$$\text{Evapotranspiration} = \frac{V(\rho_{\text{out}} - \rho_{\text{in}})}{A} \quad (9)$$



where  $\rho_{out}$  and  $\rho_{in}$  are the water vapor densities ( $\text{g m}^{-3}$ ) of the outgoing and in-coming air streams, respectively,  $V$  is the volumetric flow rate ( $\text{m}^3 \text{s}^{-1}$ ) and  $A$  is the basal chamber area ( $\text{m}^2$ ).

### 2.9. Soil water potential and soil hydraulic conductivity

Soil water potential was measured as indicated above. The values used in model simulations were calculated by interpolation of average values for the sensors above and below a given soil layer and weighted by root density in the soil layers.

The  $\alpha$ ,  $n$  and  $m$  parameters were calculated using the ROSETTA code (ROSETTA Lite V 1.0; Schaap, 1999) with values of granulometry, apparent density and water content at pressures of 0.033 and 1.5 MPa. The soil saturated hydraulic conductivity ( $K_s$ ), depicted in Fig. 1, was determined with a constant head permeameter (EMBRAPA 1997). Soil moisture release curves from a dense savanna soils obtained in the soil laboratory of the Agricultural Research Center for the Cerrado region (EMBRAPA, Brazil) are shown in Fig. 1.

### 2.10. Fine root distribution and its characteristics

Patterns of fine root distribution for the cerrado denso site were obtained from Rodin (2004). Fine root biomass decreased exponentially with increasing depth from  $4.3 \text{ Mton ha}^{-1}$ , at 10 cm depth to  $0.5 \text{ Mton ha}^{-1}$  at 100 cm (Rodin, 2004).

Maximum soil-root radial conductance ( $C_{Rmax}$ ) was considered to be the mean values between  $C_{Rmax}$  obtained by Ryel et al. (2004) in an *Artemisia tridentata* stand and  $C_{Rmax}$  obtained by Williams et al. (1996) in a *Quercus-Acer* stand.

The relative soil-root hydraulic conductance ( $c_i$ ) was estimated from transpiration and  $\Psi_{soil}$  relationships (Ryel et al., 2002, 2004). The rate of water loss from each soil layer was assumed to be directly proportional to the soil-root interface hydraulic conductance (Sperry et al., 1998; Meinzer et al., 2004). The parameters  $\Psi_{50}$  and  $b$  used in Eq. (7), and indicated in Table 3 were obtained from linear regression functions fitted to the data.

## 3. Results

Tree density, stem basal area, and tree leaf area index increased from campo sujo (open savanna) to cerrado (closed savanna or woodland) (Table 1). The leaf area index of the herbaceous layer, on the other hand, decreased from open to closed savannas. The soils are very deep oxisols with a high percentage of clay (higher than 50%; data not shown). Despite their high clay content, the soils behave like coarser-textured soils and are extremely well-drained. Mean values of soil field capacity, bulk soil density and porosity at 10 and 100 cm depth did not change substantially along the tree density gradient (Table 1). Soil water potential differences between 20 and 100 cm depth during the dry season changed along the topographic gradient from about 1.2 MPa in savannas with high herbaceous plant cover to 0.11 MPa in the cerrado with relatively low herbaceous plant cover (Table 1).

Representative diurnal courses of water storage and  $\Psi_{soil}$  for a cerrado denso site during the peak of the dry season are shown in Fig. 2. Partial recovery of water storage and  $\Psi_{soil}$  began at about 1800 h, continuing to the early morning hours and was restricted to the upper 60 cm of the soil profile. The magnitude of overnight partial recovery of soil water storage and  $\Psi_{soil}$  for the 20–60 cm soil layer was  $0.15 \text{ mm day}^{-1}$  and  $0.09 \text{ MPa day}^{-1}$ , respectively. At depths greater than 60 cm, however, water storage and  $\Psi_{soil}$  declined in a “descending staircase” pattern and late afternoon-nighttime recovery was not observed (Fig. 2). Similar patterns of water storage and  $\Psi_{soil}$  temporal variations at both soil depths were observed in the campo cerrado, but the magnitudes of the diurnal variations were larger ( $0.22 \text{ mm day}^{-1}$  and  $0.12 \text{ MPa day}^{-1}$  for the 20–60 cm soil layer, respectively).

The magnitude of partial overnight recovery of soil water storage at 20 cm during the dry season was positively correlated with variation among sites in the leaf area index of herbaceous plants and inversely correlated with total tree basal area (Fig. 3). While campo sujo and campo cerrado sites with higher cover of herbaceous plants and lower tree density exhibited rates of recovery of  $0.065$  and  $0.078 \text{ mm day}^{-1}$ , respectively, a cerrado site with the lowest ground layer LAI

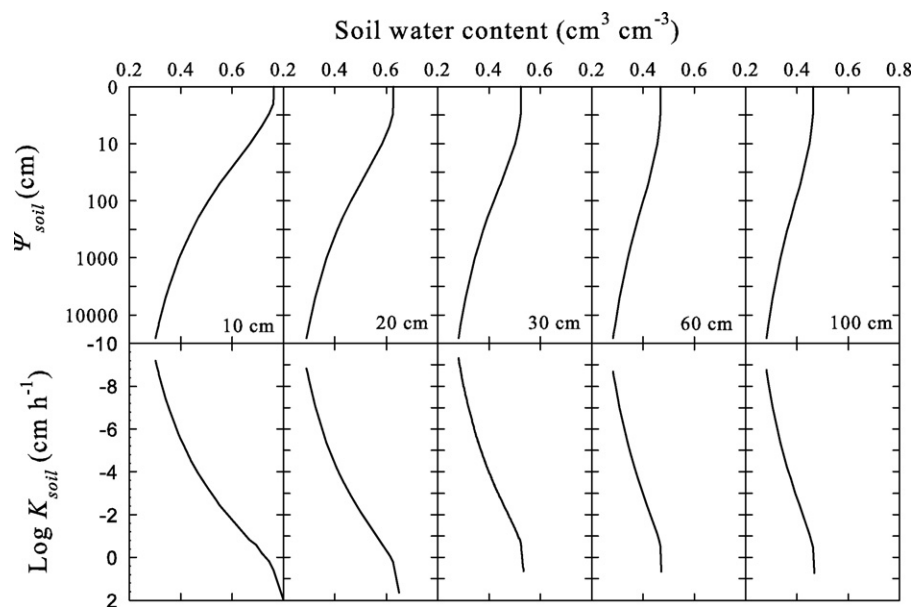


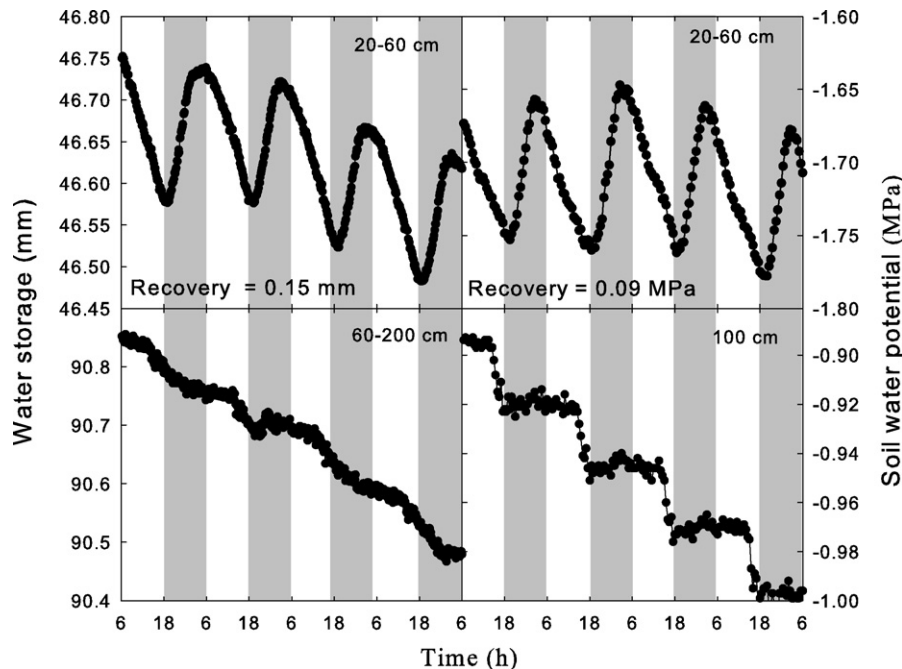
Fig. 1. Upper panels: Soil water retention curves (water potential as a function of volumetric water content;  $10200 \text{ cm} = 1 \text{ MPa}$ ) at 10, 20, 30, 60 and 100 cm depth; Lower panels: Log of non-saturated hydraulic conductivity ( $K_s$ ) in relation to water content at 10, 20, 30, 60 and 100 cm depth. Both types of information are for soils from a cerrado denso savanna.

**Table 3**

Mean daily partial decline and recovery of soil water potential ( $\Psi_{\text{soil}}$ , MPa) at 20, 30 and 60 cm depth in control and treatment plots in a campo cerrado savanna. Each value is the mean  $\pm$  SE of different days before and after removal of above ground portions of grasses and herbaceous dicots.

Depth	Control		Treatment	
	$\Psi_{\text{soil}}$ decline	$\Psi_{\text{soil}}$ recovery	$\Psi_{\text{soil}}$ decline	$\Psi_{\text{soil}}$ recovery
20 cm	$-0.23 \pm 0.02$	$-0.16 \pm 0.01$	Before $-0.23 \pm 0.01a$ After $-0.13 \pm 0.09b$	$-0.20 \pm 0.01a$ $-0.35 \pm 0.08b$
30 cm	$-0.14 \pm 0.02$	$-0.07 \pm 0.01$	Before $-0.16 \pm 0.03a$ After $-0.05 \pm 0.01b$	$-0.08 \pm 0.03$ $-0.12 \pm 0.03$
60 cm	$-0.12 \pm 0.01$	$-0.07 \pm 0.00$	Before $-0.21 \pm 0.02a$ After $-0.06 \pm 0.02b$	$-0.03 \pm 0.01a$ $-0.10 \pm 0.03b$

Different letters indicate significant differences ( $p < 0.01$ ) between before and after the treatment was applied.



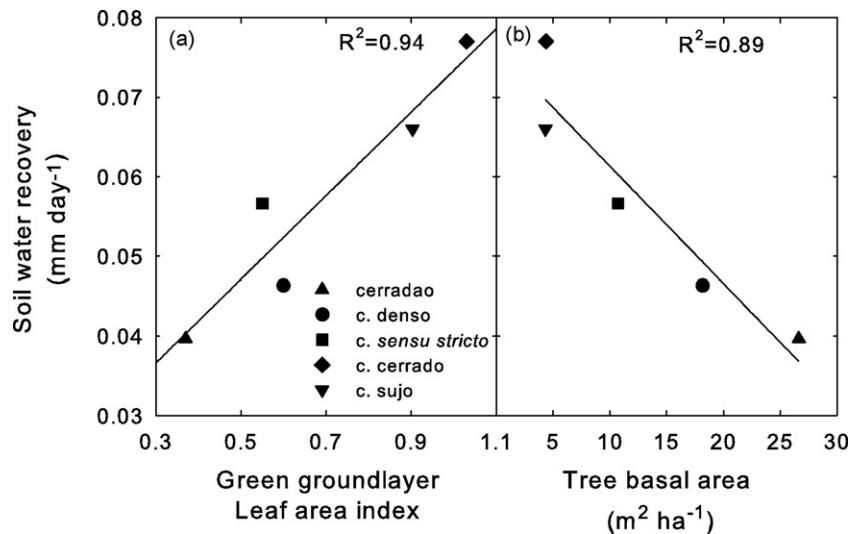
**Fig. 2.** Diel courses of soil water storage and soil water potential in a cerrado denso savanna during the dry season for two different soil layers: 20–60 and 60–200 cm depths (August 8–11, 2001). Mean daily recovery values were obtained subtracting diel minimum water storage value from subsequent diel maximum values, and by taking the absolute value of the overnight partial recovery of soil water potential.

and highest tree density showed a rate of recovery of only  $0.04 \text{ mm day}^{-1}$  (Fig. 3).

During the end of the 2006 dry season (September), when ground layer  $LAI$  in a campo cerrado was  $1.35 \text{ m}^2 \text{ m}^{-2}$ , predawn and midday leaf water potentials of herbaceous plants in the treatment plots were,  $-0.75$  and  $-1.9$  MPa, respectively. The net daily decline in  $\Psi_{\text{soil}}$  was about  $0.23$  and  $0.14$  MPa at 20 and 30 cm, respectively, and diel partial recovery was about  $0.16$  and  $0.07$  MPa at 20 and 30 cm, respectively (Table 3 and Fig. 4). Diurnal oscillations in soil water potentials were larger in the upper soil layers compared to deeper soil layers (Fig. 4). There were not only diurnal variations of soil water potential but there was also a continuous decline over time. Before the treatment,  $\Psi_{\text{soil}}$  was more negative in shallow soil layers compared to deeper soil layers: The mean initial  $\Psi_{\text{soil}}$  was  $-0.91 \pm 0.22$  MPa at 20 cm,  $-0.61 \pm 0.19$  MPa at 30 cm,  $0.54 \pm 0.16$  MPa at 60 cm and  $-0.035 \pm 0.00$  MPa at 100 cm depth. The aboveground biomass of all herbaceous plants was removed from the treatment plots on September 19th to eliminate the ground-layer transpiration. Immediately after the treatment, the trends of declining  $\Psi_{\text{soil}}$  were reversed at 20, 30 and 60 cm: mean  $\Psi_{\text{soil}}$  in the treatment plots increased with time, indicating that the amount of water stored in the upper soil layers increased. No

treatment response was observed at 100 cm depth (Fig. 4). Leaf water potential of trees responded to the treatment: while average predawn and midday  $\Psi_L$  were  $-0.66 \pm 0.05$  MPa and  $-1.75 \pm 0.35$  MPa respectively before the ground layer removal, after removal of the ground layer the average predawn and midday  $\Psi_L$  were  $-0.53 \pm 0.03$  MPa and  $-1.62 \pm 0.33$  MPa, respectively ( $n = 3-5$ ).

Simulated temporal variation in the magnitude of hydraulic lift and of non-saturated water flow ( $NSF$ ) from June 5 to August 13, a period without precipitation, showed that the magnitude of  $NSF$  declined at the beginning of the dry season (Fig. 5a). Soil water potential ( $\Psi_{\text{soil}}$ ) on June 5 (early dry season) ranged from  $-0.45$  MPa to about  $0$  MPa (data not shown), depending on soil depth. Non-SF contributed 8% to the partial daily recovery of  $\Psi_{\text{soil}}$  at the beginning of the dry season with its contribution decreasing to near zero after 20 days of drought. On the other hand, the magnitude of hydraulic lift increased to a maximum of  $0.7 \text{ mm day}^{-1}$  after 20 days and then declined until August 13, when  $\Psi_{\text{soil}}$  ranged from  $-2.34$  to  $-1.46$  MPa between 10 and 100 cm soil depth (results not shown) (Fig. 5a). The contribution of hydraulic lift to overnight recovery of soil water storage in the 20–60 cm layer was initially 92% and reached 100% after 20 days of drought. Even though the absolute magnitude of hydraulic lift declined after



**Fig. 3.** Relationship between (a) soil water storage recovery at 20 cm depth and ground layer green leaf area index and (b) soil water storage recovery and tree basal area during September 2003 in five savanna sites with different tree density. All values of green ground layer leaf area index (LAI) are from grasses and herbaceous dicots.

reaching its maximum, its contribution to the partial recovery of soil water storage remained at 100% because the contribution of NSF to partial recovery was zero until the end of the dry season. The simulated daily recovery of water storage between 10 and 100 cm soil depth from June 5 to August 13 resulting from the combined effect of NSF and hydraulic lift also increased initially, despite the rapid decline of NSF, until it reached a maximum after 20 days of drought (Fig. 5b). The combined recovery declined for the remainder of the dry season in parallel with the decline in the contribution of hydraulic lift to the upward movement of soil water.

Model simulations of hydraulic lift and NSF as a function of  $\Psi_{\text{soil}}$  and time elapsed into a rainless period (June 5 to August 13) yielded different trajectories of the two processes for each soil layer between 10 and 100 cm (Fig. 6a and b). For example, the upper soil layers tended to receive a larger amount of water hydraulically lifted from deeper soil layers at a given value of  $\Psi_{\text{soil}}$  than the lower soil layers. The  $\Psi_{\text{soil}}$  at maximum rates of hydraulic lift also differed among soil layers with maximum hydraulic lift occurring at about  $-1.1$  MPa at 10 cm and  $-0.8$  MPa at 30 cm. In contrast, the amount of water moved by NSF was greater in deeper soil layers compared to upper soil layers. The model also predicted that the maximum amount of water contributed by hydraulic lift would be attained earlier in the dry season in upper soil layers compared to deeper layers (Fig. 6b). Predicted NSF not only increased with depth, but its contribution to maintaining soil water content persisted longer than in the upper soil layers (Fig. 6d).

Hydraulic lift in a cerrado denso savanna slowed the rate of decline in  $\Psi_{\text{soil}}$  during the dry season, particularly in the upper soil layers (Fig. 7). For example, with hydraulic lift (Fig. 7c)  $\Psi_{\text{soil}}$  at 10 cm dropped from an initial value of about  $-0.5$  MPa to about  $-2.0$  MPa after 70 days of drought (Fig. 7c), whereas without hydraulic lift,  $\Psi_{\text{soil}}$  at 10 cm would have dropped to  $-3.8$  MPa after 70 days of drought (Fig. 7b). The effect of hydraulic lift on the rate of decline in  $\Psi_{\text{soil}}$  was smaller for soil layers at 60 and 100 cm below the surface. Non-saturated water flow had a relatively small effect on the rate of seasonal decline in  $\Psi_{\text{soil}}$ .

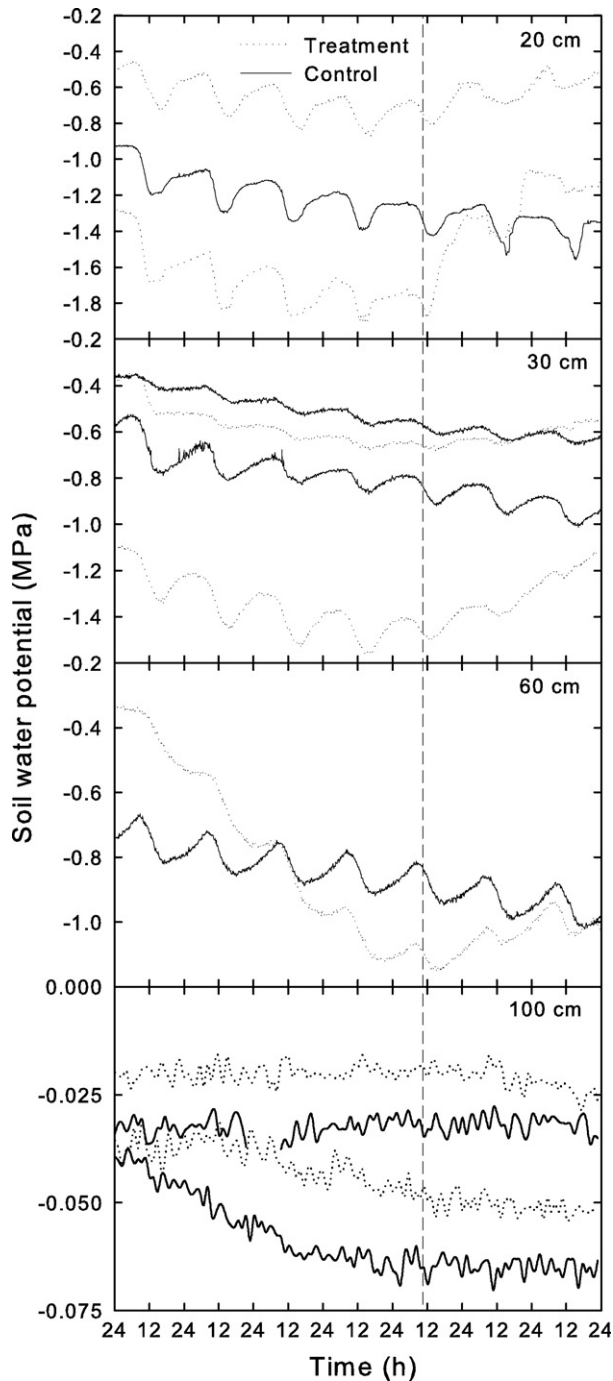
#### 4. Discussion

We have shown in previous studies that the occurrence of reverse sap flow in lateral roots of deciduous and brevidiciduous

Cerrado tree species during the dry season was consistent with hydraulic lift (Scholz et al., 2002, 2008; Moreira et al., 2003). We have also shown that water hydraulically lifted by Cerrado trees helps maintain the hydraulic conductivity of their shallow lateral roots during the dry season (Scholz et al., 2008). The contribution of trees to partial overnight recovery of soil water storage via hydraulic lift depends on their density in a given site. According to Scholz (2006), savanna trees release about 0.004 mm of water per day to the upper soil layers via hydraulic lift in a campo cerrado increasing to 0.008 mm per day in a denser savanna site (cerrado denso). This amount of hydraulically lifted water by trees and released into the upper soil layers, however, was not large enough to result in a partial overnight recovery and hence in substantial diurnal variations in soil water content and soil water potentials in the upper soil horizons (Moreira et al., 2003; Meinzer et al., 2004; Scholz et al., 2008, and this study). The only other candidates for generating such large oscillations in soil water potentials by the release of hydraulically lifted water from their shallow roots are herbaceous plants (grasses and dicots), that have a large abundance of fine roots in the upper 100 cm of soil (Oliveira et al., 2005), and/or non-saturated water flow. In the present study, the main empirical evidence for estimating the impact of the herbaceous layer on soil water availability during the dry season was the differential recovery of soil water storage as a consequence of hydraulic lift, which was higher in sites with a larger cover of a ground layer. Consequently, the changes in soil water recovery should have been mainly caused by variations in the abundance of herbaceous plants. Results from the manipulative experiment and from model simulations provided additional supporting evidence that hydraulic lift by herbaceous plants contributes substantially to the increases in the amount of water in the upper soil layers observed during the late afternoon and nighttime hours, and that the vertical water movement within the soil driven by non-saturated water flow was negligible during most of the dry season.

##### 4.1. Manipulative experiment

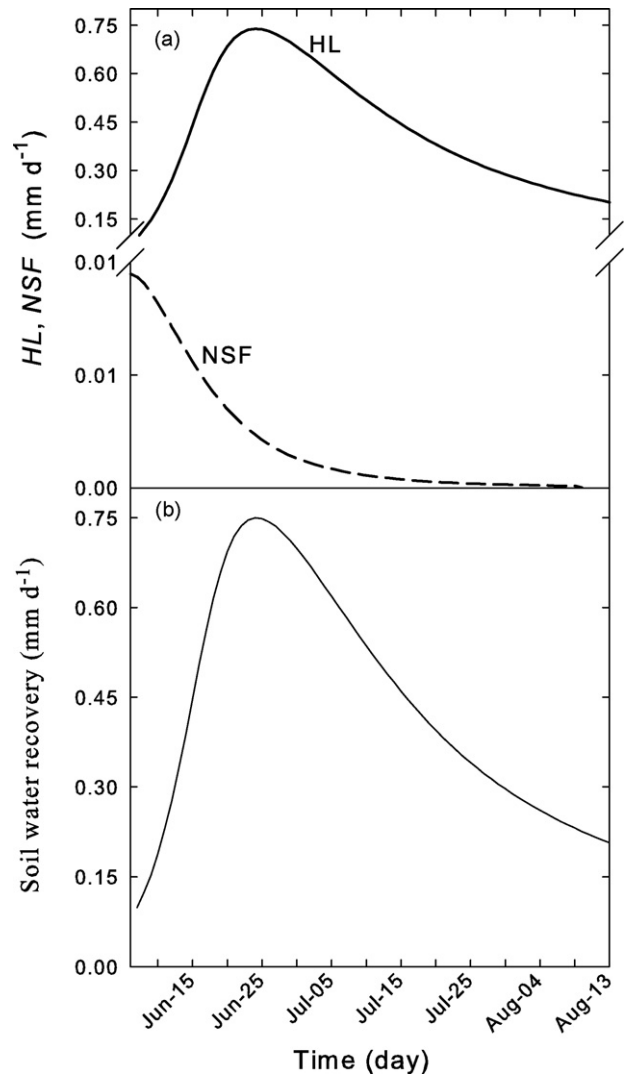
In the present study, removal of the above ground portion of herbaceous vegetation eliminated a competing sink for hydraulically lifted water allowing it to be released into the dry upper soil layers by shallow-lateral roots instead of being immediately lost as transpiration. As a consequence, overnight recovery of  $\Psi_{\text{soil}}$  was enhanced and mean  $\Psi$  in the upper soil layers became less negative



**Fig. 4.** Soil water potentials at 20, 30, 60 and 100 cm depth in a campo cerrado site, in treatment and control plots from September 15, 2006 to September 21, 2006. On September 19 (dashed line) the above ground non-woody biomass was removed from a 15 m<sup>2</sup> area in each treatment plot. Soil water potentials were measured psychrometrically. Measurements from two malfunctioning psychrometers installed at 20 and 60 cm depth in a control plot and one installed at 60 cm depth in a treatment plot are not shown.

following the treatment, consistent with an increase in the amount of water transported into the upper soil layers by hydraulic lift. However, these observations alone are not indicative of the relative impact of the herbaceous layer versus woody plants on the magnitude of hydraulic lift and its effect on the diel and longer term fluctuations in soil water potential.

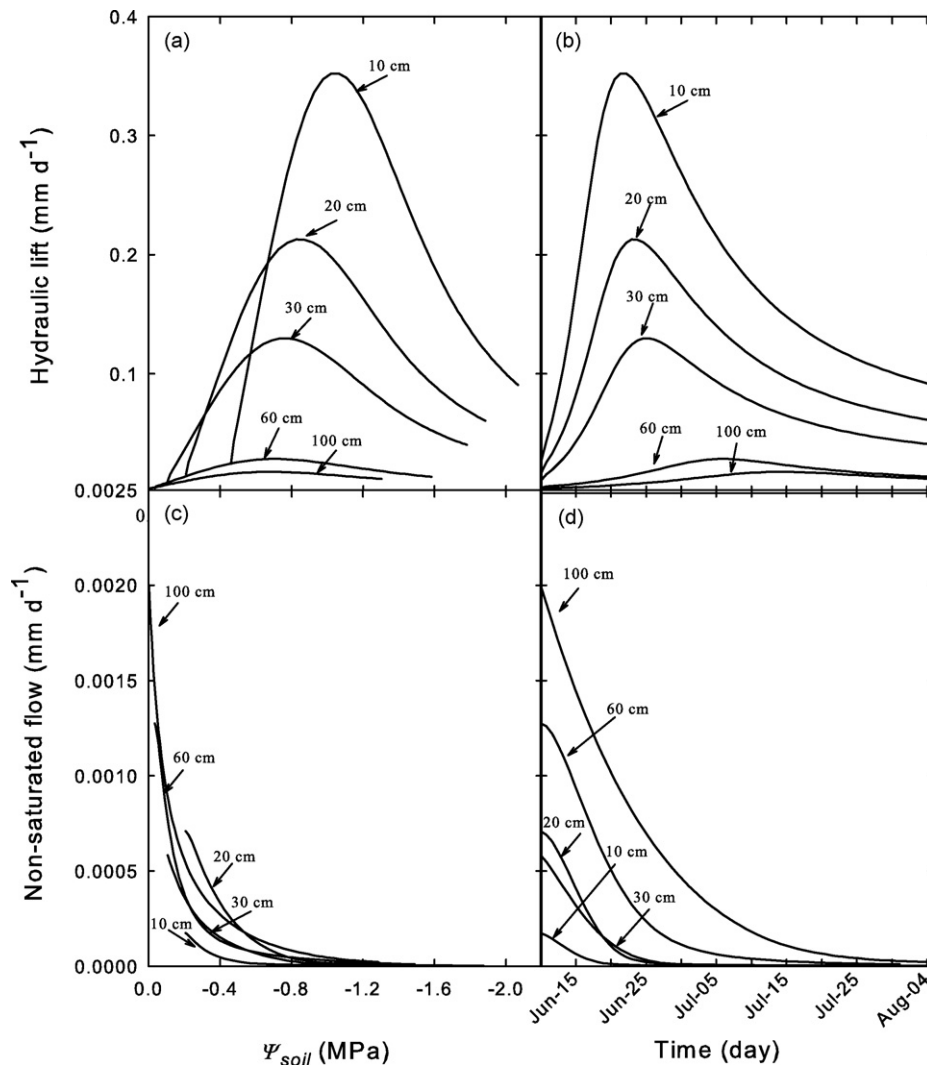
The experimental manipulations were performed around the middle of the dry season in a savanna site when a relatively large



**Fig. 5.** (a) Simulated temporal variations in the magnitude of hydraulic lift (*HL*) and of non-saturated water flow (*NSF*) and (b) temporal variation in soil water recovery between 10 and 100 cm soil depth, during the dry season of 2003. Results of model simulation are for a period without precipitation (June 5 to August 13 2003). On June 5 (early dry season) soil water potentials ranged from  $-0.45$  to about  $0$  MPa, depending on soil depth. On August 13, soil water potentials ranged from  $-2.34$  to  $-1.46$  MPa.

amount of herbaceous biomass was still active. The amount of green biomass in Cerrado vegetation declines over time during the dry season, largely as a result of extensive dieback of the herbaceous vegetation (Hoffmann et al., 2005). Previous studies have shown that roots of senescent annual grasses and plants without aboveground tissue can still redistribute large quantities of water, resulting in soil water potential increases during periods without precipitation (Leffler et al., 2005). Results of the present study suggest that decreases in the amount of green herbaceous biomass over time reduce the strength of this competing sink for water hydraulically lifted from deeper soil layers to the upper soil horizons because sites with high abundance of herbaceous plants have higher rates of recovery of  $\Psi_{\text{soil}}$  compared to sites with low abundance of herbaceous plants. Overnight recovery of  $\Psi_{\text{soil}}$  at 20 cm depth at the end of the dry season (August) was relatively low in sites with low leaf area index of herbaceous plants, such as in cerradão sites, suggesting that root systems of herbaceous plants are at least partially responsible for soil water content recovery. Similarly, Scholz (2006) found that the magnitude of overnight





**Fig. 6.** Simulated changes in hydraulic lift (a, b) and non-saturated flow (c, d) for five soil depths as a function of decrease in soil water potential for each layer and time elapsed into a rainless period during the dry season. The estimates of hydraulic lift and non-saturated flow were obtained with the simulation model using parameters in Table 2 and root distributions described in Rodin (2004).

partial recovery of soil water storage and  $\Psi_{\text{soil}}$  was substantially greater in a campo cerrado site with a large abundance of herbaceous plants, than in a cerrado denso site, during the middle of the dry season. The reduced magnitude of diel variation in  $\Psi_{\text{soil}}$  after removal of the aboveground biomass of herbaceous plants further suggests that herbaceous plants are responsible for a major portion of hydraulic lift in the Cerrado.

#### 4.2. Model simulations

The model was able to effectively predict diel and seasonal changes in  $\Psi_{\text{soil}}$  during the dry season in the study site. Simulations were conducted to compare model calculations of  $\Psi_{\text{soil}}$  with measured  $\Psi_{\text{soil}}$  for a 5-day period during the dry season. Both the diurnal changes in  $\Psi_{\text{soil}}$  and the decline in  $\Psi_{\text{soil}}$  with time were well described by the model. The linear relationship between measured and predicted values of  $\Psi_{\text{soil}}$  from all soil layers for the 5-day period ( $n = 4$  depths, 5 days, 48 measurements per day) had an  $R^2$  of 0.94 with a slope and intercept that were not statistically different from 1 to 0 respectively ( $p < 0.001$ ,  $y = 0.90x - 0.06$ ).

Predicted soil water recovery increased at the beginning of the dry season, consistent with increases in contributions of hydraulic lift to the upper soil layers. However, rates of hydraulic lift peaked relatively early in the dry season causing

overnight recovery of soil water storage to decline sharply toward the end of the dry season (Fig. 5). It is possible that declining soil water content increased soil-root interface resistance, which could impede release of hydraulically lifted water into the drier soil layers. Small decreases in radial and axial root hydraulic conductance from the wet to dry season were observed in a previous study of woody savanna plants that perform hydraulic lift (Domec et al., 2006; Scholz et al., 2008). The increase in the water potential gradient between shallow and deep soil apparently did not fully compensate for the seasonal loss of hydraulic conductivity in lateral roots (Warren et al., 2007). Thus, partial root rectification (Scholz et al., 2008) may explain the drop in the contribution of hydraulic lift to upper soil layers during the last part of the dry season, as predicted by the model. Differences in the vulnerability of roots to cavitation may also explain the  $\Psi_{\text{soil}}$  at which maximum values of hydraulic lift were attained (e.g. maximum hydraulic lift was reached at about  $-1.1$  MPa at 10 cm while at 30 cm it was reached at  $-0.8$  MPa). Roots tapping water from deeper soil are more vulnerable to cavitation than shallow roots (Domec et al., 2006). The ability of the shallow roots to avoid cavitation at relatively negative soil water potentials may help them to absorb water and acquire nutrients during the dry season from the upper soil layers where most nutrients are located.

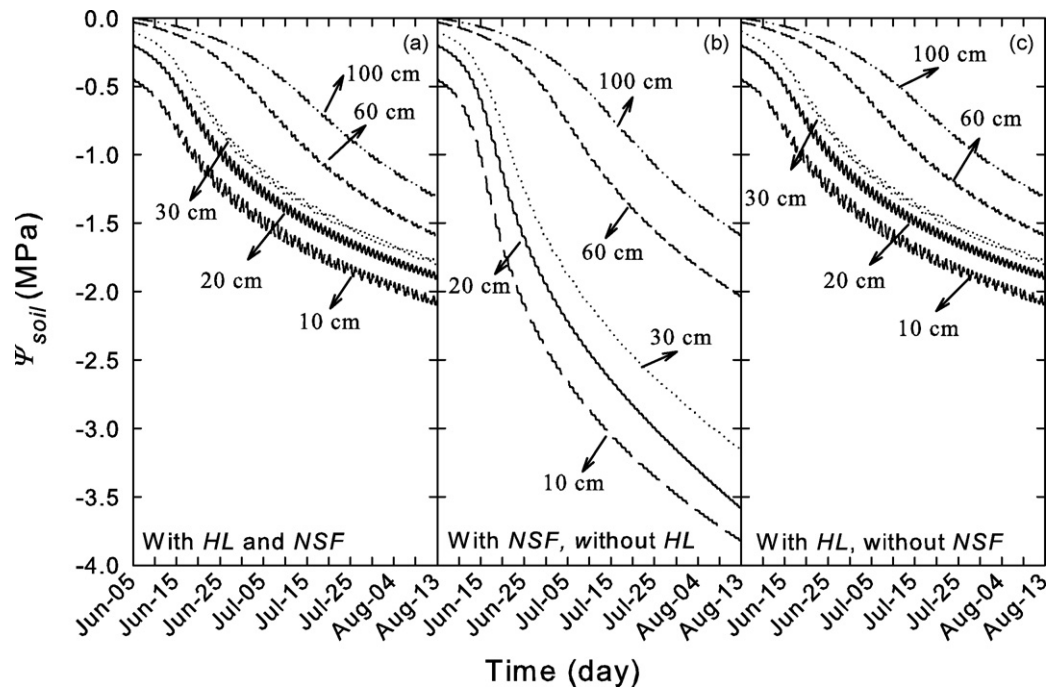


Fig. 7. Simulated soil water potentials at five soil depths over a 70-day period (June 5 to August 13) for a cerrado denso savanna using parameters in Table 2 and fine root distribution from Rodin (2004), (a) with hydraulic lift and non-saturated flow, (b) non-saturated flow without hydraulic lift and (c) hydraulic lift without non-saturated flow.

From the standpoint of soil water balance, the model simulations suggested that hydraulic lift substantially affected the rate of decline in  $\Psi_{\text{soil}}$  during the dry season (Fig. 7). With hydraulic lift,  $\Psi_{\text{soil}}$  in the upper 10 cm would have dropped to about  $-2.0$  MPa during the latter part of the dry season, whereas without hydraulic lift (but with NSF),  $\Psi_{\text{soil}}$  would have dropped to  $-3.8$  MPa. Consequently, hydraulic lift reduced the seasonal decline in bulk  $\Psi_{\text{soil}}$  by 1.8 MPa, which may have helped to avoid complete hydraulic failure in shallow roots. Domec et al. (2006) observed that Cerrado roots lose their water transport capacity at  $\Psi_{\text{soil}}$  below  $-3$  MPa. Avoiding substantial xylem cavitation in shallow roots should promote the rapid recovery of plant activity after the first rains in the dry to wet season transition period.

In a recent study, we used eddy-covariance measurements to estimate and compare the energy balance and evapotranspiration in Cerrado sites differing in tree density. The average evapotranspiration for the dry season months of June, July and August in a cerrado denso site was  $1.81 \text{ mm day}^{-1}$  (Giambelluca et al., 2009). According to model simulations, the daily recovery of soil water storage in the upper 100 cm associated with hydraulic lift was on average  $0.42 \text{ mm day}^{-1}$  during the same period, which represents 23% of the total site-specific evapotranspiration measured by eddy-covariance methods in a cerrado denso. Consequently, hydraulic lift appears to have an important ecosystem level impact on water cycling in Brazilian savannas. It is likely that in the absence of hydraulic lift, water deficits, particularly in herbaceous plants, would have been substantially larger. Increased water deficits and therefore earlier dieback of herbaceous plants during the dry season, would likely lead to increased fire frequency, which would affect ecosystem dynamics and the balance between herbaceous and woody plants in the Cerrado.

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#### References

- Brown, R.W., Bartos, D.J., 1982. A calibration model for screen-caged peltier thermocouple psychrometers. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. Research paper INT-293.
- Bucci, S.J., Scholz, F.G., Goldstein, G., Hoffmann, W.A., Meinzer, F.C., Franco, A.C., Giambelluca, T., Miralles-Wilhelm, F., 2008. Controls on stand transpiration and soil water utilization along a tree density gradient in a Neotropical savanna. *Agricultural and Forest Meteorology* 148, 839–849.
- Domec, J.C., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., Villalobos-Vega, R., 2006. Diurnal and seasonal variation in root xylem embolism in Neotropical savanna woody species: impact on stomatal control of plant water status. *Plant, Cell and Environment* 29, 26–35.
- Franco, A.C., Bustamante, M., Caldas, L.S., Goldstein, G., Meinzer, F.C., Kozovitz, A.R., Rundel, P., Coradin, V., 2005. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees* 19, 326–335.
- Giambelluca, T.M., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., Hoffmann, W.A., Franco, A.C., Buchert, M.P., 2009. Evapotranspiration and energy balance of Brazilian savannas with contrasting tree density. *Agricultural and Forest Meteorology* 149, 1365–1376.
- Goodland, R., 1971. A physiognomic analysis the Cerrado vegetation of Central Brazil. *Journal of Ecology* 59, 411–419.
- Haridasan, M., 2000. Nutrição mineral das plantas nativas do Cerrado. *Brazilian Journal of Plant Physiology* 12, 54–64.
- Hoffmann, W.A., Silva, E., Machado, G., Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., 2005. Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. *Oecologia* 145, 307–316.
- Hutley, L.B., O'Grady, A.P., Eamus, D., 2000. Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. *Functional Ecology* 141, 83–194.
- Jury, W.A., Gardner, W.R., Gardner, W.H., 1991. *Soil Physics*, Fifth edition. John Wiley & Sons, Inc., New York, 328 p.
- Leffler, A.J., Peek, M.S., Ryel, R.J., Ivans, C.Y., Caldwell, M.M., 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* 86, 633–642.
- Lenza, E., Klink, C.A., 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Revista Brasileira de Botânica* 29, 627–638.
- Meinzer, F.C., Brooks, J.R., Bucci, S.J., Goldstein, G., Scholz, F.G., Warren, J.M., 2004. Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types. *Tree Physiology* 24, 919–928.
- Moreira, M.Z., Scholz, F.G., Bucci, S.J., Sternberg, L.S., Goldstein, G., Meinzer, F.C., Franco, A.C., 2003. Hydraulic lift in a Neotropical savanna. *Functional Ecology* 17, 573–581.
- Mualem, Y., 1976. A new model for predicting the hydraulic conductivity of unsaturated porous media. *Water Resources Research* 12, 513–522.
- Nobel, P.S., Sanderson, J., 1984. Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* 35, 727–737.
- Oliveira, R.S., Beserra, L., Davidson, E.A., Pinto, F., Klink, C.A., Nepstad, D.C., Moreira, A., 2005. Deep root function in soil water dynamics in cerrado savanna of central Brazil. *Functional Ecology* 19, 574–581.

- Paltineanu, I.C., Starr, L.L., 1997. Real-time soil water dynamics using multisensor capacitance probes laboratory calibration. *Soil Science Society American Journal* 61, 1381–1393.
- Quesada, C.A., Miranda, A.C., Hodnett, M.G., Santos, A.J.B., Miranda, H.S., Breyer, L.M., 2004. Seasonal and depth variation of soil moisture in a burned open savanna (campo sujo) in central Brazil. *Ecological Applications* 14, 533–541.
- Quesada, C.A., Hodnett, M.G., Breyer, L.M., Santos, A.J.B., Andrade, S., Miranda, H.S., Miranda, C., Lloyd, J., 2008. Seasonal variations in soil water in two woodland savannas of central Brazil with different fire history. *Tree Physiology* 28, 405–415.
- Rodin, P., 2004. Distribucao da biomasa subterranea e dinamica de raices finas em ecossistemas nativos e em uma pastagem plantada no Cerrado do Brasil Central. M.S. Thesis. University of Brasilia, Brazil.
- Ryel, R.J., Caldwell, M.M., Poder, C.K., Or, D., Leffler, A.J., 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130, 173–184.
- Ryel, R.J., Leffler, A.J., Peek, M.S., Ivans, C.Y., Caldwell, M.M., 2004. Water conservation in *Artemisia tridentata* through redistribution of precipitation. *Oecologia* 143, 335–345.
- Schaap, M.G., 1999. ROSETTA code. United States Department of Agriculture. Agricultural Research Service. United States Salinity Laboratory, Riverside, CA.
- Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., 2002. Hydraulic redistribution of soil water by *Neotropical savanna* trees. *Tree Physiology* 22, 603–612.
- Scholz, F.G., 2006. Biofísica del transporte de agua en el sistema suelo-planta: redistribución, resistencias y capacitancias hidráulicas. Ph.D. Thesis. Universidad de Buenos Aires, Argentina, p. 79.
- Scholz, F.G., Bucci, S.J., Goldstein, G., Moreira, M.Z., Meinzer, F.C., Domec, J.-C., Villalobos-Vega, R., Franco, A.C., Miralles-Wilhelm, F., 2008. Biophysical and life history determinants of hydraulic lift in *Neotropical savanna* trees. *Functional Ecology* 22, 773–786.
- Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* 25, 251–263.
- Tomasella, J., Hodnett, M.G., 1997. Estimating unsaturated hydraulic conductivity of Brazilian soils using soil water retention data. *Soil Science* 162, 703–712.
- van Genuchten, M.T., 1980. A closed form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal* 44, 893–898.
- Warren, J.M., Meinzer, F.C., Brooks, J.R., Domec, J.C., Coulombe, R., 2007. Hydraulic redistribution of soil water in two old-growth coniferous forests: quantifying patterns and controls. *New Phytologist* 173, 753–765.
- Williams, M., Rastetter, E.B., Fernandes, D., Goulden, M.L., Wofsy, S.C., Shaver, G.R., Melillo, J.M., Munger, J.W., Fan, S.-M., Nadelhoffer, K.J., 1996. Modeling the soil-plant atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment* 19, 911–927.