

Biophysical and life history determinants of hydraulic lift in Neotropical savanna trees

F. G. Scholz^{*1,2}, S. J. Bucci^{1,2}, G. Goldstein^{3,4}, M. Z. Morelra⁵, F. C. Melnzer⁶, J.-C. Dornec⁷, R. Villalobos-Vega⁸, A. C. Franco⁹ and F. Miralles-Wilhelm¹⁰

¹Leboretorio de Ecologia Funcional, Departamento de Biología, Universidad Nacional de la Patagonia San Juan Bosco, (9000) Comodoro Rivadavia, Argentina; ²Comision Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; ³Laboratorio de Ecologia Funcional, Universidad de Buenos Aires, Ciudad Universitaria, Buenos Aires, Argentina; ⁴Department of Biology, University of Miami, Florida, USA; ⁵Centro de Energia Nuclear na Agricultura (CENA), Piracicaba, SP 13416-903, Brazil; ⁶USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331, USA; ⁷Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina 27795 USA; ⁸Department of Biology, University of Miami, Florida 33124, USA; ⁹Departamento de Botanica, Universidade de Brasilia, Brasilia, OF 70904-970, Brazil; and ¹⁰Department of Civil and Environmental Engineering, Florida International University, EC 3680, Miami, Florida 33174, USA

Summary

1. Ecological and physiological characteristics of vascular plants may facilitate or constrain hydraulic lift. Studies of hydraulic lift typically include only one or few species, but in species-rich ecosystems a larger number of representative species needs to be studied.

2. Measurements of sap flow in tap roots, lateral roots and stems, as well as stable isotope labelling techniques were used to determine the occurrence and relative magnitude of hydraulic lift in several individuals of nine co-occurring Brazilian savanna (Cerrado) tree species differing in life-history traits, and to assess physical and biological determinants of this process at the tree and ecosystem level.

3. The occurrence of reverse sap flow observed in deciduous and brevideciduous species during the dry season was consistent with hydraulic lift. The evergreen species did not exhibit reverse flow. Consistent with their ability to carry out hydraulic lift, the brevideciduous and deciduous species had both shallow and tap roots (dimorphic root systems), whereas the evergreen species had mostly deep roots (monomorphic root systems).

4. In the deciduous and brevideciduous species, the contribution of tap roots to transpiration increased substantially as the dry season progressed. Seasonal changes in the contribution of tap roots to transpiration were not observed in the evergreen species.

5. There was an inverse relationship between rates of reverse sap flow and seasonal loss of hydraulic conductivity in lateral roots, suggesting that hydraulic lift in Cerrado woody plants may help maintain the functionality of the lateral roots in exploring dry and nutrient rich superficial soil layers without directly enhancing the amount of water uptake.

6. Reverse sap flow in lateral roots of the deciduous and brevideciduous species increased asymptotically as the driving force for water movement from roots to the soil increased. This nonlinear relationship implies that additional sinks for water such as nocturnal transpiration and refilling of internal water storage tissues may compete for internal water resources during the dry season.

7. There appears to be a trade-off between greater year-round access to nutrients in the upper soil layers (deciduous and brevideciduous species) and a greater access to deep and more reliable water sources during the dry season (evergreen species), which has implications for whole-ecosystem water, carbon and nutrient balance in Neotropical savannas.

Key-words: hydraulic redistribution, leaf phenology, nocturnal transpiration, root architecture, root conductivity

*Correspondence author. E-mail: fgscholz@unpata.edu.ar

Introduction

Hydraulic lift involves the passive transport of soil water from relatively wet deep soil layers to drier surface layers through root systems (Richards & Caldwell 1987; Caldwell & Richards 1989), and usually occurs at night when the xylem water potential (Ψ) of the above-ground part of the plant and upper roots rises above that of the upper soil layers. Hydraulic redistribution has been suggested as a more general term for this process because water movement can occur from upper to lower soil layers or laterally depending on the direction of the soil water potential gradient (Burgess *et al.* 1998; Smith *et al.* 1999). Hydraulic lift will be used hereafter unless water transport is downward. Additional requirements for hydraulic lift are root systems that explore soil layers with different water potentials and a relatively low resistance to reverse sap flow (negative sap flow) for water moving out of the roots into dry soil. Ecological, physiological and hydraulic characteristics of vascular plants may facilitate or impose constraints on hydraulic lift. Among these factors, seasonal leaf area dynamics, night-time transpiration, timing of use and recharge of internal water storage, root architecture, and patterns of stomatal conductance could influence the magnitude of hydraulic lift.

It is believed that hydraulic lift can contribute significantly both to the water balance of the plants responsible for it and that of neighbouring plants of the same or other species (Dawson 1993; Moreira *et al.* 2003). Water released from roots into drier soil layers may be re-absorbed when transpiration exceeds water uptake by deep roots alone (Richards & Caldwell 1987). In addition to improving plant water balance during periods with low precipitation, hydraulic lift may also enhance nutrient uptake by fine roots located in the relatively nutrient rich portion of the soil profile, which normally undergoes desiccation in environments characterized by a pronounced dry season (Caldwell, Dawson & Richards 1998), and may help to maintain the activity of mycorrhizae (Querejeta, Egerton-Warburton & Allen 2003, 2007; Plamboeck *et al.* 2007; Warren *et al.* 2008).

Tropical savannas are the second most extensive vegetation type in South America, and among them, the Cerrado of central Brazil forms the largest regional system (Goodland 1971). Cerrado communities are characterized by high tree species diversity (Sarmiento 1984). More than 500 species of trees and large shrubs are present within savanna ecosystems in the Cerrado region (Ratter *et al.* 1996), and even relatively small areas may contain up to 70 or more species of vascular plants (Felfili *et al.* 1998). 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 (e.g. Hill 1969; Medina 1982; Cochrane 1989). The low relative humidity and relatively high daytime temperatures in the Cerrado impose a consistently high evaporative demand during the prolonged dry season. During this period, water in the upper soil layers is severely depleted as evidenced by the dieback of grasses (Hotfmann *et al.* 2005) and by the low water potential (more negative) in the upper

portion of the soil profile (Franco 1998), while deeper layers retain high water content even after several months without rain (Quesada *et al.* 2004, 2008). These environmental conditions fulfil the requirements for hydraulic lift to occur (e.g. Scholz *et al.* 2002; Moreira *et al.* 2003; Meinzer *et al.* 2004).

Studies of hydraulic lift usually involve one or very few species from a particular site or vegetation type (e.g. Richards & Caldwell 1987; Burgess *et al.* 2001; Brooks *et al.* 2002; Ludwig *et al.* 2003; Hultine *et al.* 2003). To establish the prevalence of this phenomenon in species-rich ecosystems, a larger number of representative species needs to be studied. In the present work, members of three different woody plant functional groups characterized by their leaf phenology were studied to understand the prevalence of hydraulic lift and its ecological consequences in species-rich Cerrado ecosystems. In previous research using non-invasive stable isotope techniques, it was found that root systems of deciduous Cerrado species tended to tap deeper sources of soil water during the dry season than roots of evergreen species (Jackson *et al.* 1999), leading us to hypothesize that the occurrence and magnitude of hydraulic lift may differ among woody species with different seasonal patterns of leaf area dynamics.

Nine dominant evergreen, brevideciduous, and deciduous woody species were selected for this study. Our objectives were to (i) determine associations between leaf phenology and root system architecture and the occurrence of hydraulic lift among Cerrado woody species, (ii) assess other biophysical factors (recharge of stem storage, root conductance and rectification and nocturnal transpiration) governing hydraulic lift in Cerrado tree species, and (iii) identify some potential ecosystem level effects of hydraulic lift in Cerrado vegetation types. To attain our objectives, we measured stem and root sap flux in several trees using heat pulse techniques, leaf, root and soil water potentials, air saturation deficits, and hydraulic conductivities (total, radial and axial) of shallow roots. In addition we performed experimental manipulations such as feeding of deuterated water to tap roots and covering the crown of trees to prevent transpiration.

Materials and methods

SITE DESCRIPTION AND PLANT MATERIAL

Cerrado vegetation comprises five physiognomic savanna types ranging from *cerradão*, woodland with a closed or semi-closed canopy, to *campo sujo*, an open savanna with scattered trees and shrubs. The present study was conducted in *cerrado denso* and *campo cerrado* savannas with intermediate tree density (*cerrado denso* savanna with basal area of $18.2 \text{ m}^2 \text{ ha}^{-1}$ and *campo cerrado*, an open tree and shrub savanna with basal area of $4.4 \text{ m}^2 \text{ ha}^{-1}$). Cerrado vegetation contains different combinations of these savanna types organized spatially along gradients of decreasing abundance of woody plants from *cerradão* to *campo sujo* over distances of only a few km. The study was conducted at the Instituto Brasileiro de Geografia e Estatística (IBGE) research station located 33 km south of Brasília ($15^\circ 56' \text{S}$, $47^\circ 53' \text{W}$, altitude 1100 m) between August 2000 and January 2004. 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. The soils are nutrient poor and well drained deep oxisols.

Nine species among the 25 woody species with the highest measured importance value indices (Felfili *et al.* 1994) were selected for the study. *Sclerolobium paniculatum* Vog. (Leguminosae) is an evergreen tree up to 10-m-tall with compound pinnate leaves, containing four to six large leaflets. *Schefflera macrocarpa* (Seem.) D.C. (Araliaceae) is an evergreen tree up to 10-m-tall with palmately compound leaves on branches clustered near the apex of the stem. *Vochysia elliptica* Mart. (Vochysiaceae) is an evergreen tree species up to 7-m-tall with simple leaves and short petioles. *Byrsonima crassa* Nied. (Malpighiaceae) is a brevideciduous shrub or tree up to 5-m-tall with large scleromorphic simple leaves. *Blepharocalyx salicifolius* (H.B. & K.) Berg. (Myrtaceae) is a brevideciduous tree up to 10-m-tall with small simple leaves. *Dalbergia miscolobium* Benth. (Leguminosae) is a brevideciduous tree up to 12-m-tall with compound leaves and 5 to 10 pairs of small leaflets. *Qualea parviflora* Mart. (Vochysiaceae) is a deciduous small tree with simple opposite leaves. *Kielmeyera coriacea* (Spr) (Clusiaceae) Mart. is a deciduous tree with simple alternate leaves and short petioles; and *Aspidosperma tomentosum* Mart. (Apocynaceae) is a deciduous tree up to 15-m-tall with large scleromorphic simple leaves.

Root systems of representative individuals of the nine dominant tree species were excavated to study their architectural features, such as the number of lateral roots and their length, and the presence or absence of a main tap root. Leaf phenology, height, basal area, and number of individuals per species whose roots were excavated are indicated in Table 1.

ENVIRONMENTAL VARIABLES AND SOIL AND ROOT WATER POTENTIAL

Relative humidity and air temperature were monitored continuously with probes (HMP35C, Campbell Scientific, Logan, UT) placed at 12 m and 4 m in height for *cerrado denso* and *campo cerrado*, respectively, near the center of the study sites. Data were obtained every 10 s, and averaged every 10 min averages were recorded with a datalogger (CR 10X, Campbell Scientific, Logan, UT). Air saturation deficit (*D*) was calculated as the difference between saturation vapour pressure at the air temperature and ambient vapour pressure.

Soil psychrometers (pST-55, Wescor, Logan, UT) were used to continuously monitor soil water potential (Ψ_{soil}) at 10, 20, 30, 60 and 100 cm depth. A soil auger was used to excavate four 1-m-deep holes, and the psychrometers were inserted through the lateral walls of the

holes into the intact soil profile. The holes were then carefully repacked with the excavated soil. Four psychrometers profile were spaced out across a representative 300-m² area in the vicinity of trees differing in leaf phenology. 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 with a 30-s cooling time and data were recorded with a datalogger (CR-7, Campbell Scientific) and corrected for potential temperature gradients according to Brown & Bartos (1982). Psychrometer cables and dataloggers were insulated to minimize temperature gradients that could influence water potential measurements.

Leaf water potential was measured with a pressure chamber (PMS, Albany OR). Leaf samples were immediately sealed in plastic bags upon excision and kept in a cooler until balancing pressures were determined in the laboratory within 1 h of sampling collection. Covered leaf water potential was measured on leaves enclosed in plastic bags and wrapped in aluminium foil at dusk prior to the measurement day to prevent nocturnal water loss. Covered leaves make it possible for the water potential in the leaf xylem to be in equilibrium with that of stem xylem at the point of attachment of the petiole (Simmoneau & Habib 1991). Measurements of water potential were done in three to five leaves per tree (three species and three individuals per species) at dawn. Root water potential (Ψ_{root}) was estimated from the Ψ of covered leaves (Domec *et al.* 2006).

SAP FLOW MEASUREMENTS

Sap flow was measured using a modified heat pulse technique on the excavated central tap root, on one or more lateral roots, and on the trunk base (Burgess *et al.* 1998; Scholz *et al.* 2002) in three to ten trees of each of the nine species (evergreen, brevideciduous and deciduous) indicated above. On some trees we installed heat pulse systems on all the major roots to quantify water uptake from different layers of the soil profile during the different seasons. Lateral and tap roots were exposed by manually excavating a pit with a radius of c. 0.75 m centred on the main trunk. Extreme care was taken to avoid damaging the roots. Heat pulse probes were installed in tap roots and in 1- to 3-cm-diameter lateral roots c. 10–30 cm from the main trunk. Sap flow was monitored continuously for 3–10 days with the exceptions indicated below. The root region where the probes were installed was covered with soil to decrease daily temperature fluctuations. When negative flows were observed, zero flow offset values were determined at the end of the measurement period by severing the proximal and distal ends of a root section containing probes, thereby isolating it from the rest of the plant (Scholz *et al.*

Table 1. Leaf phenology, height, diameter of the main stem and number of excavated individuals per species for determining root architecture. Tree height and basal diameter are expressed as mean $\pm$ SE ($n = 3$ to 15)

Species	Leaf phenology	Height (m)	Basal diameter (cm)	Number of trees
<i>Schefflera macrocarpa</i>	Evergreen	3.9 $\pm$ 0.2	11.2 $\pm$ 0.9	6
<i>Sclerolobium paniculatum</i>	Evergreen	6.0 $\pm$ 0.3	15.3 $\pm$ 1.1	4
<i>Vochysia elliptica</i>	Evergreen	4.0 $\pm$ 0.2	5.1 $\pm$ 0.1	5
<i>Byrsonima crassa</i>	Brevideciduous	2.1 $\pm$ 0.1	9.0 $\pm$ 0.4	35
<i>Blepharocalyx salicifolius</i>	Brevideciduous	4.0 $\pm$ 0.1	9.6 $\pm$ 0.6	35
<i>Dalbergia miscolobium</i>	Brevideciduous	4.2 $\pm$ 0.3	12.6 $\pm$ 1.3	5
<i>Aspidosperma tomentosum</i>	Deciduous	3.2 $\pm$ 0.3	4.4 $\pm$ 0.3	5
<i>Kielmeyera coriacea</i>	Deciduous	2.6 $\pm$ 0.2	5.6 $\pm$ 0.5	35
<i>Qualea parviflora</i>	Deciduous	2.6 $\pm$ 0.2	5.2 $\pm$ 0.3	25

2002). Calculations pertaining to the heat pulse method are described in Burgess *et al.* (1998) and Scholz *et al.* (2002). Heat pulse sensors were connected to roots and stems of three individuals per species (*A. tomentosum*, *B. crassa*, *B. salicifolius* and *K. coriacea*) from the beginning of the dry season (late May) until the end of the dry season (late August) to assess the effect of soil-root water potential gradients and nocturnal transpiration on hydraulic lift. Three individuals of *B. crassa* and two individuals of *K. coriacea* were studied during the dry season until the beginning of the wet season to test if downward hydraulic redistribution occurs in Cerrado ecosystems.

DEUTERIUM LABELLING AND ISOTOPE ANALYSIS

Tap roots of deciduous and brevideciduous trees with reverse sap flow were cut one or two days after the heat pulse probes were installed in roots and stems. The first cut was at c. 0.75 m below the root crown. Tap roots were re-cut under water 0.25 m above the first cut to avoid air entry that would induce embolism. The tap roots were fed with 75% D₂O solutions in calibrated containers that permitted total volumetric uptake to be recorded. Samples of roots and soil around the roots were taken 8 days after feeding deuterated water to the tap root and upon termination of sap flow measurements. The objective of this experiment was to corroborate that shallow roots of trees with reverse flow were actually releasing water into the dry soil. Samples were obtained in the morning and sealed in Vacutainer tubes (7 mL, Becton Dickinson, NJ) for water extraction with vacuum distillation and isotopic analyses. Soil and lateral root samples of control plants were collected.

Samples were taken to the laboratory for water extraction and analysis of their deuterium content by mass spectrometry according to Moreira, Sternberg & Nepstad (2000). Hydrogen isotope ratios (δD) are expressed as deviation in parts per thousand from the international standard Vienna-standard mean ocean water (V-SMOW). To determine background abundances of deuterium in the soil and roots, samples were collected from and around control trees located > 50 m from individuals fed with deuterated water.

ROOT HYDRAULIC CONDUCTIVITY

Total hydraulic conductivity (L_p), radial hydraulic conductivity (L_R) and axial hydraulic conductivity (K_h) were measured in roots collected between 0530 and 0700 h in January–2004 and August 2004. Four species with different magnitudes of reverse sap flow were selected for measurements of root conductivity (*B. crassa*, *B. salicifolius*, *K. coriacea* and *Q. parviflorai*). Root segments c. 25-cm-long and 2–4 mm in diameter were excised and immersed in distilled water. In the laboratory, a 15-cm-long section of each root was re-cut under water, and the bark and cambium were removed from a 1 cm region at the proximal end. The exposed portion was inserted into 5-mm Tygon tubing attached to a glass capillary half filled with distilled water. The Tygon tubing was sealed firmly to the outer sapwood by tightening a compression fitting. The distal cuts ends were sealed with cyanoacrylate adhesive. Water flow through the roots was induced by applying a partial vacuum (–10 to –50 kPa) to the open end of the attached capillary while the root segments were immersed under distilled water. The pressure was adjusted by a needle valve and monitored using a digital manometer (Cole-Parmer® 68603, Vernon Hills, IL). A pipette capable of resolving 0.01-mm³ and a magnifying glass were used to observe the location of the meniscus, and the distance travelled by the meniscus along the capillary per unit time was used to calculate the volumetric flow rate (Q_v , m³ s^{–1}).

When Q_v became constant at a given pressure (P , MPa), root hydraulic conductivity, L_p (m S^{–1} MPa^{–1}) was calculated as:

$$L_p = (\Delta Q_v / \Delta P) / (1/A)$$

where A (m²) is the lateral surface area of the root segment (Nobel, Schulte & North 1990).

Radial conductance was equated to the volumetric flux density of water (m S^{–1}) at the root surface divided by the difference in water potential (MPa) from the root surface to the root xylem. Root radial hydraulic conductivity average over the root segment (L_R , m S^{–1} MPa^{–1}) was calculated as:

$$L_R = L_p \alpha / \tanh(\alpha L)$$

where α (m^{–1}) is $(2\pi r_{\text{root}} L_p / K_h)^{1/2}$, r_{root} (m) is the radius of root segment (Landsberg & Fowkes 1978) and K_h is axial conductivity, L_R was initially set equal to L_p and was then gradually increased to solve the equation for L_R by iteration.

To measure axial conductivity (K_h) used to calculate L_R , the distal end of the root segment was cut and its terminal 2-mm portion was re-cut under distilled water. Then K_h (m⁴ S^{–1} MPa^{–1}) was calculated as:

$$K_h = Q_v / (\Delta P / L)$$

where ΔP (MPa) is the pressure drop, and L (m) is the length of the root segment. Q_v was measured as for L_p .

Results

There were two rainless months (June and July) during the dry season of 2003, the main study period, and the mean air saturation deficit (D) increased by about 1 kPa between the beginning and the end of the dry season (Fig. 1a). Consistent with the reduced water input from precipitation and increased evaporative demand, soil water potentials decreased substantially during the dry season. In August 2003 soil water potentials were –2.2 and –1.5 MPa at 20 and 100 cm deep, respectively (Fig. 1b). The insert in Fig. 1b depicts daily time courses of soil water potential (Ψ_{soil}) at 30 and 100 cm deep between 6 and 10 August 2003. There were noticeable daily fluctuations at 30 cm depth without substantial longer term changes, but Ψ_{soil} at 100 cm depth decreased in a nearly continuous manner.

Diel patterns of root and stem sap flux (gm^{–2}s^{–1}) during the dry season differed in the three group of species. Five out of the six deciduous and brevideciduous species exhibited reverse (negative) sap flux in at least one lateral root (Fig. 2a–e). One of the brevideciduous species (*D. miscolobium*, panel f) did not exhibit reverse sap flux in the roots studied, and none of the evergreen species exhibited reverse sap flux in their roots (Fig. 2 g–i). Reverse sap flux typically occurred at night, but in one root of *K. coriacea* reverse sap flux occurred during the daytime as well (Fig. 2a). The maximum reverse sap flux measured was –5.2 g m^{–2} s^{–1} for the deciduous species and –16.3 g m^{–2} s^{–1} for the brevideciduous species (data not shown).

Patterns of seasonal variations in sap flux differed among species depending on their leaf phenology (Fig. 3). None of the species studied exhibited reverse sap flux in lateral roots

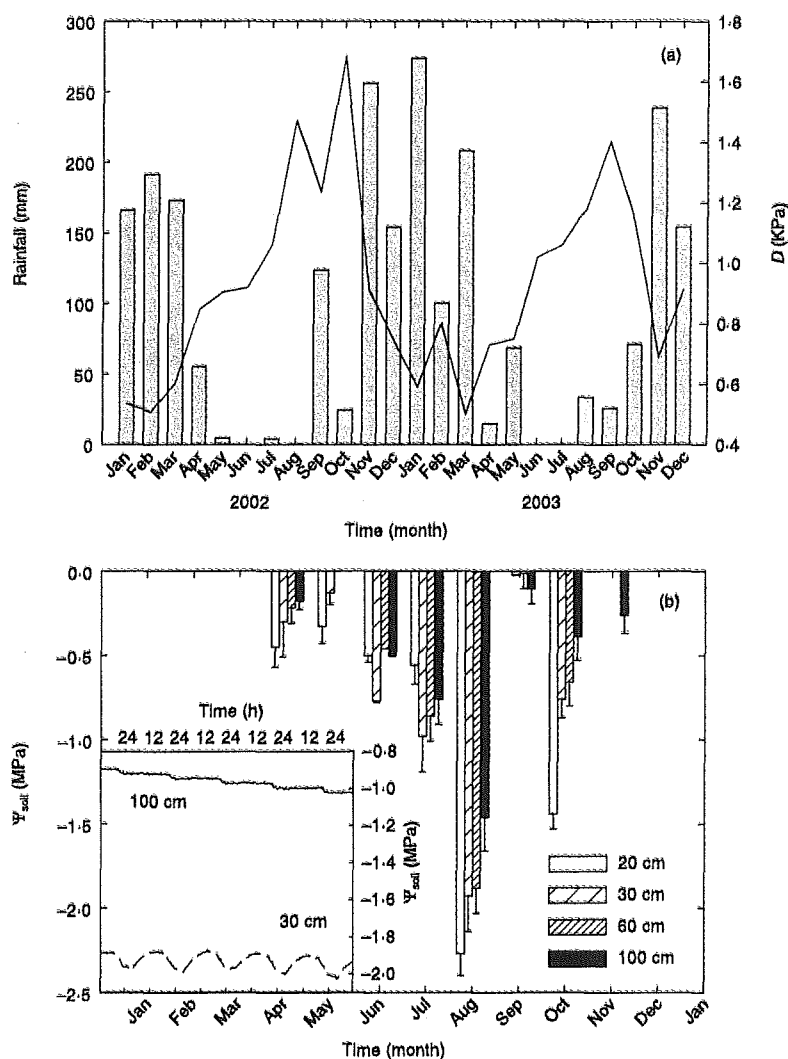


Fig. 1. Seasonal variation in mean monthly (a) precipitation and air saturation deficit (D) from January 2002 to December 2003, and (b) soil water potential at 20, 30, 60 and 100 cm depth, for several days of the 2003 dry season at the IBGE research station. The insert in panel (b) shows typical diurnal fluctuations of soil water potential for 5 days at the end of the dry season (August) at 30 and 100 cm depth. Bars in panel (a) represent precipitation and the solid line represents D . Bars in panel (b) are mean monthly values ($\pm$ SE) of four replicate sensors per depth during 3 or 4 days per month.

during the wet season, but as the dry season progressed, *K. coriacea* and *B. crassa*, deciduous and brevidciduous species respectively, exhibited reverse sap flux in their lateral roots, particularly at the end of the dry season. Reverse sap flux was not detected in lateral roots of the evergreen species *S. macrocarpa* and no substantial decrease in stem or root sap flow occurred during the dry season (Fig. 3 and Table 2). On the other hand, the maximum sap flux for stems and lateral roots decreased toward the end of the dry season in the deciduous and brevidciduous species. Consistent with this decline in sap flux in trunks and lateral roots, the tap root contribution to total daily sap flow in the deciduous and brevidciduous species increased toward the end of the dry season (Table 2). In contrast, the contribution of the tap root to the total daily trunk sap flow in the evergreen *S. macrocarpa* did not change significantly from wet to dry season (Table 2).

Diagrammatic representations of root distribution for Cerrado trees that hydraulically lift water, and for species or individuals that do not perform hydraulic lift are represented in Fig. 4. In some cases one species may have individuals that

fit more than one diagrammatic model of root architecture. Potential differences in root architecture within one species are expected due to the heterogeneity of nutrient distribution within the soil profile and of soil physical properties that may modify root growth patterns. Overall, species that showed hydraulic lift had dimorphic root systems with active roots exploring several soil layers, while species that did not perform hydraulic lift tended to have monomorphic root systems with roots that tap water from similar soil layers.

With the exception of one lateral root in *Q. parviflora* and one in *B. crassa*, all lateral roots sampled contained water with $3D$ values higher than background values found in roots obtained from control plants (Fig. 5a). The deuterium label was not only observed in the lateral roots but also in the soil around the roots of treated plants (Fig. 5b). All soil water samples, except one from around the lateral root of a *B. crassa* plant, had $3D$ values higher than the background, indicating that the deuterated water fed to the tap root moved into the soil around the roots of treated plants by reverse sap flow through lateral roots.

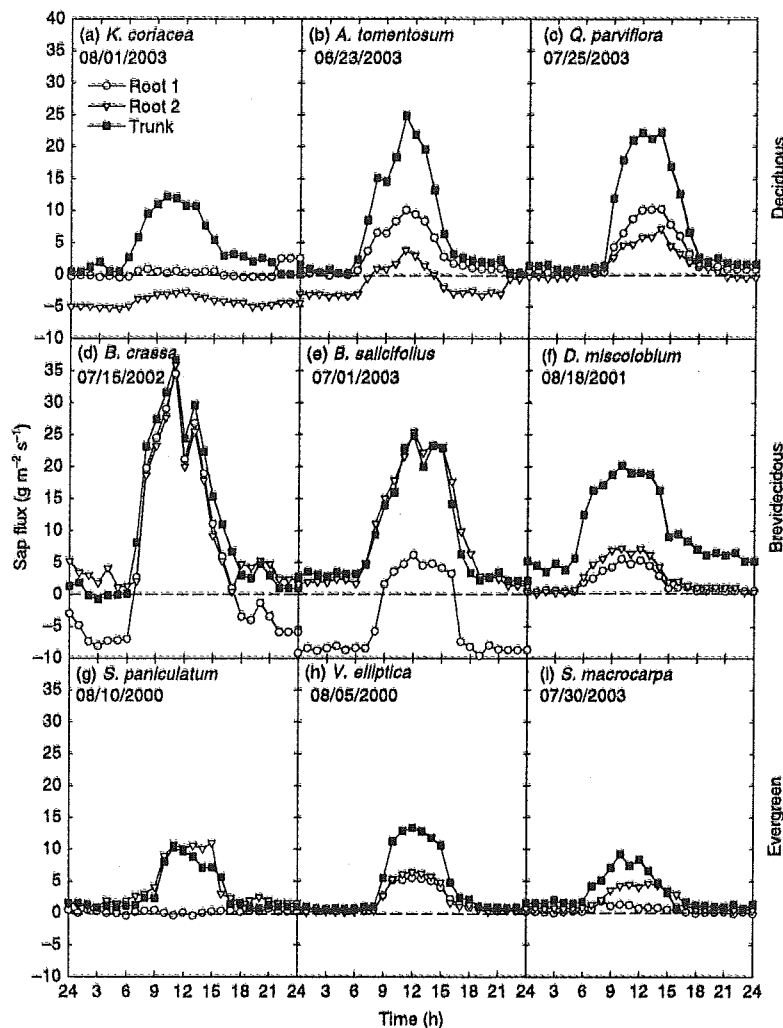


Fig. 2. Typical daily courses of sap flux in the main stem and two roots of a single representative individual of three dominant deciduous (a, b, c), three brevideciduous (d, e, f) and three evergreen (g, h, i) Cerrado woody species during the dry season. Positive sap flux values indicate water movement toward the leaves and negative values (reverse sap flux) indicate water movement from the root to the soil.

Reverse sap flow in lateral roots of deciduous and brevideciduous species capable of hydraulic lift increased asymptotically as the difference in water potential between roots and soil increased (Fig. 6). When the Ψ_{soil} to Ψ_{root} difference reached a threshold of about 0.8 MPa, the reverse sap flow did not respond to any further increases in the driving force for water movement (Fig. 6). Reverse sap flow in lateral roots of deciduous and brevideciduous species also increased asymptotically with increasing percentage of nocturnal sap flow through the main stem (Fig. 7). At the end of the dry season, when nocturnal basal sap flow represent a relatively large fraction of the total daily sap flow (20–30%), reverse flow in lateral roots tended to remain constant. The percent loss of total and radial hydraulic conductivity (L_R) in lateral shallow roots during the wet to dry season transition decreased linearly with increasing reverse sap flux in lateral roots across four species studied (Fig. 8a,b).

The total leaf surface area in a deciduous tree (*K. coriacea*) appeared to have an effect on the number of lateral roots undergoing reverse sap flow (Fig. 9). Reverse sap flux was only

observed in one lateral root at night time when *K. coriacea* still had a full crown of leaves during the middle of the dry season (Fig. 9a). However, after the same tree became leafless one month later, all the roots studied exhibited reverse sap flux (Fig. 9b). Sap flux was barely detectable in the main stem at this time. A similar pattern of sap flux was observed in a *K. coriacea* tree with leaves when transpiration was prevented experimentally (Fig. 9c). During the dry to wet season transition, different diel patterns of sap flux were observed depending on rainfall and soil moisture. At the end of the dry season, when the soil water potential of the upper soil layer (10 cm) was about 1.2 MPa more negative than the soil water potential at 100 cm depth, one lateral root of *B. crassa* exhibited reverse sap flow at night as expected (Fig. 10a). Two days later, the water potential of the upper soil layers increased to 0 MPa as a consequence of a 17 mm rain event (Fig. 10b). Despite soil water potential gradients that should have favoured reverse flow from the main stem to deeper roots or from shallow roots to tap roots at night, both the lateral and tap roots showed positive sap flux. The maximum stem

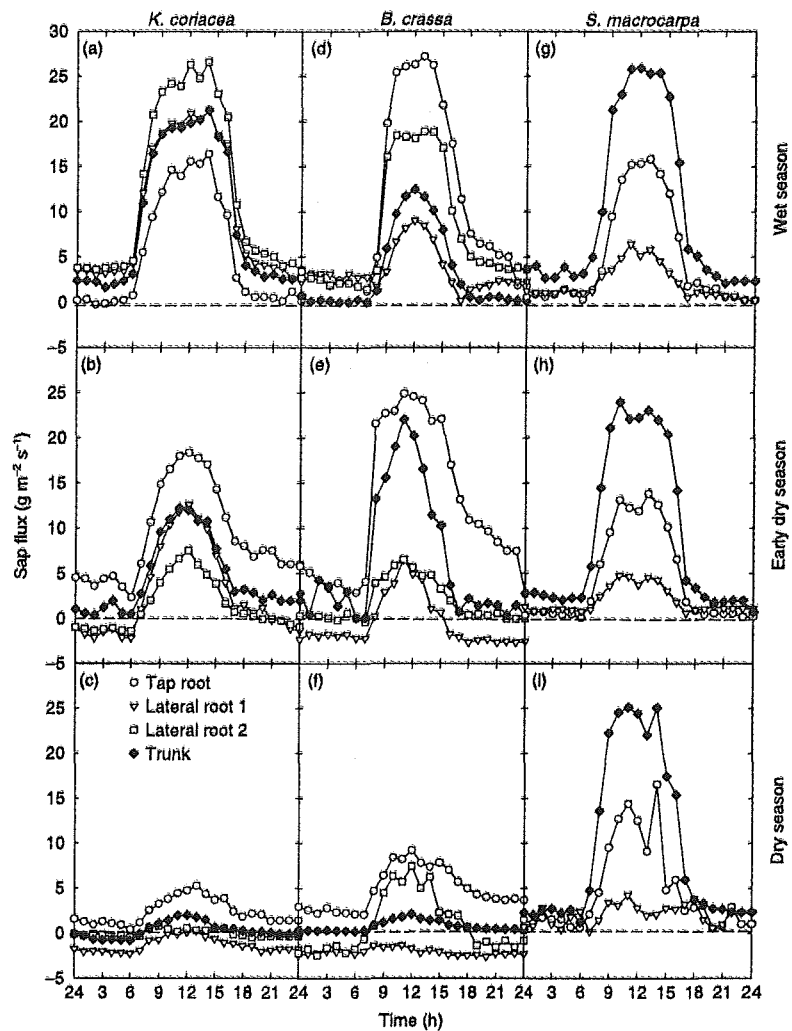


Fig. 3. Representative seasonal variation in sap flux in the main stem, tap root and lateral roots of *K. coriacea*, a deciduous species (a, b, c), *E. crassa*, a brevideciduous species (d, e, f) and *S. macrocarpa*, an evergreen species (g, h, i) from the wet season (November 2002), early dry season (June 2003) and at the peak of the dry season (August 2003).

Table 2. Seasonal variation in sap flow ($\text{cm}^3 \text{ day}^{-1}$) in the trunk, one lateral root and the tap root of one representative individual of *K. coriacea*, *E. crassa* and *S. macrocarpa*. Negative values of sap flow indicate reverse flow (from root to soil). For *K. coriacea* and *E. crassa*, the positive and reverse (negative) sap flow values, in lateral roots, are indicated separately for the early dry season and dry season, respectively. Values in parentheses represent the percentage of lateral or tap root total daily sap flow compared to the trunk total daily sap flow

		Sap flow ($\text{cm}^3 \text{ day}^{-1}$)		
		Wet season	Early dry season	Dry season
<i>K. coriacea</i> deciduous	Trunk	1140	577	149
	Lateral root	264 (23%)	3.8 (0.7%) -3.5 (0.6%)	3.8 (2.5%) -3.9 (2.6%)
	Tap root	156 (13%)	273 (47%)	70 (47%)
<i>B. crassa</i> brevideciduous	Trunk	553	336	128
	Lateral root	27 (4.9%)	8.8 (2.6%) -13.5 (4%)	-15.6 (12%)
	Tap root	166 (30%)	124 (37%)	75 (58.6%)
<i>S. macrocarpa</i> evergreen	Trunk	1286	1192	1243
	Lateral root	486 (37.8%)	407 (34.1%)	419 (33.8%)
	Tap root	237 (18.4%)	207 (17.4%)	200 (16.1%)

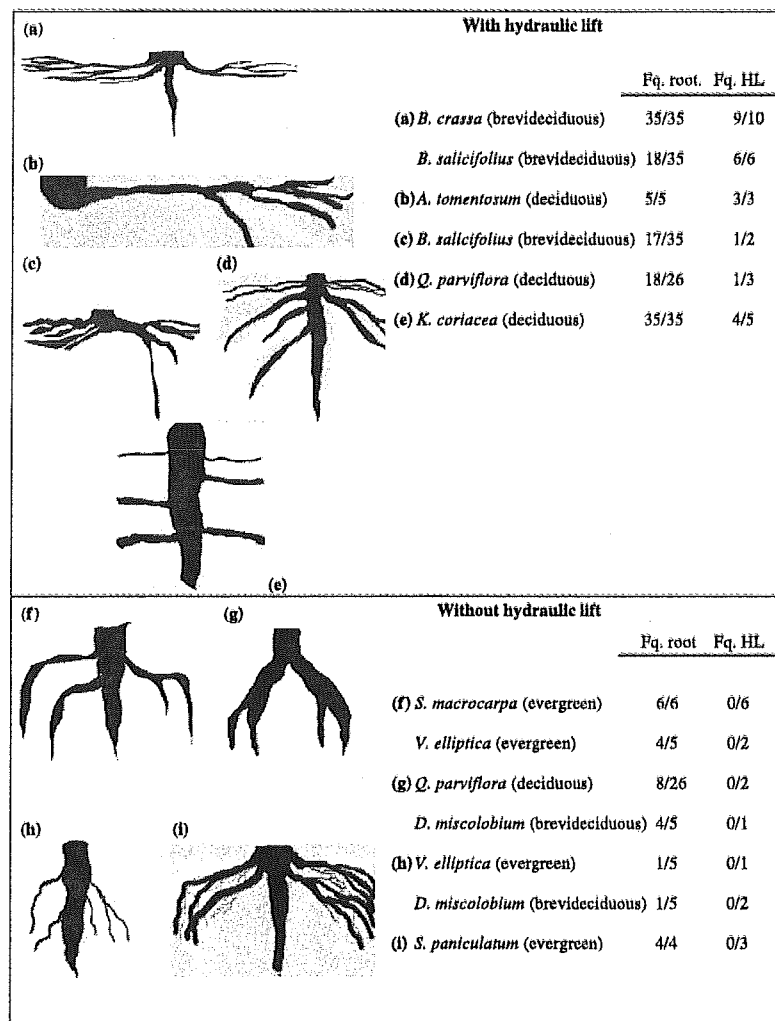


Fig. 4. Diagrammatic representations of root architecture in Cerrado trees for species or individuals that hydraulically lift water (a-e) and for species or individuals that did not show evidence of hydraulic lift (f-i). The frequency of individuals with that particular type of root system architecture/total number of studied individuals (Fq. root) and the frequency of individuals exhibiting hydraulic lift/total number of individuals studied (Fq. HL) are indicated. Major active roots, either tap roots or lateral roots with secondary growth that are easily observed during an excavation, are represented.

sap flux density during the day was relatively low due to low vapour pressure deficit. Eleven days later, when soil water potential was zero from the soil surface down 1 m due to several rain fall events, all root fluxes at night were very close to zero or slightly positive, typical for roots during the wet season (Fig. 10c).

DISCUSSION

RELATIONSHIPS BETWEEN HYDRAULIC LIFT, SPATIAL PATTERNS OF ROOT DISTRIBUTION AND LEAF PHENOLOGY

Root systems that explore deep soil layers or large soil volumes are a prerequisite for sustaining transpiration and carbon fixation during periods of low soil water availability in seasonally dry environments. Cerrado trees in particular, allocate more than 50% of their biomass below-ground (Castro & Kauffman 1998) and explore large soil volumes, with several species having very deep roots (e.g. Rawitscher

1948; Jackson *et al.* 1999; Oliveira-Filho *et al.* 1994; Sarmiento, Goldstein & Meinzer 1985; Goldstein, Sarmiento & Meinzer 1985; Meinzer *et al.* 1999; Bucci *et al.* 2005; Franco *et al.* 2005). Nevertheless the broader functional significance of different patterns of root distribution and their impact on whole ecosystem processes is still poorly understood.

Consistent with differences in their root architecture (monomorphic vs. dimorphic root systems), seasonal changes in the temporal patterns of sap flow differed among species depending on their leaf phenology. As the dry season progressed, deciduous and brevid deciduous species exhibited reverse sap flow in their lateral roots, particularly at the end of the dry season, and the contribution of tap roots to transpiration increased substantially. In this sense, deciduous and brevid deciduous species showed, facultative behaviour, using a substantial amount of water from deep soil layers during the dry season (up to 57% of total daily water use) and shallow soil water during the rainy season. The evergreen species did not have 'true' lateral roots with reverse sap flow, and did not show any substantial change in the partitioning of root flow

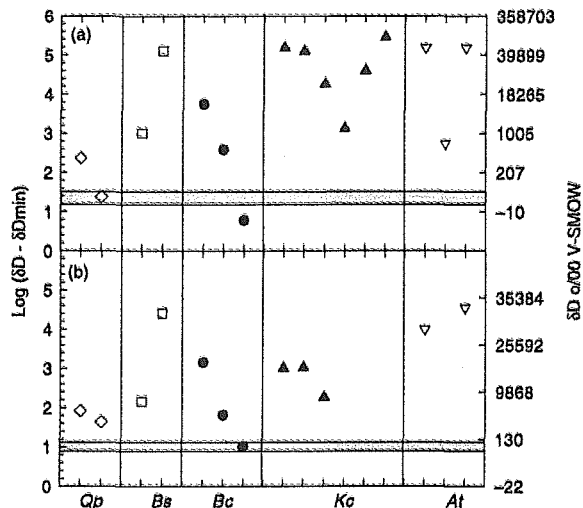


Fig. 5. (a) Log of difference between the hydrogen isotope ratio (δD) of water obtained from lateral roots of the treated plants (tap root supplied with deuterated water) and δD of root water (δD_{min}) from the control plants whose tap roots were not supplied with deuterated water, and (b) Log of difference between δD of soil water around the roots of the treated plants and δD of soil water around roots of control plants (δD_{min}). Actual δD values equivalent to those indicated on the log scale are shown on the right axis. Soil and root water with δD values within the grey area are not significantly different from values of control plants; those outside the grey area are significantly different from values of control plants at $P < 0.1$. The species studied were: Qp: *Qualea parviflora* ($\diamond$), Bs: *Blepharocalyx salicifolius* ($\square$), Bc: *Byrsonima crassa* ($\circ$), Kc: *Kielmeyera coriacea* (Δ) and At: *Aspidosperma tomentosum* (∇).

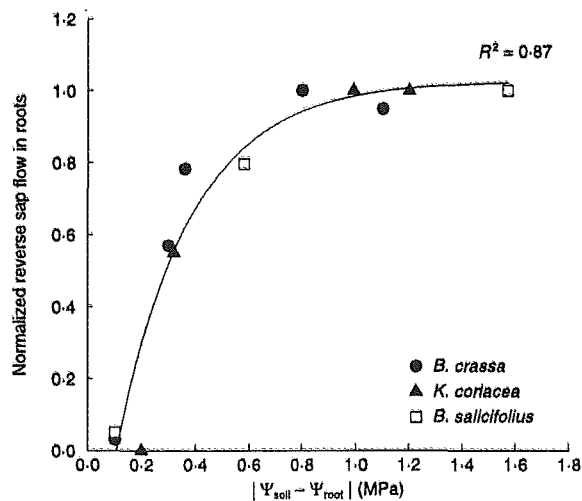


Fig. 6. Normalized total daily reverse sap flow in lateral roots of three woody species in relation to the absolute value of the difference between soil and root water potential ($|\Psi_{soil} - \Psi_{root}|$) for different days between the beginning and end of the dry season of 2003. Reverse sap flow was normalized respect to the maximum value reached for a particular root during the dry season. Values of Ψ_{soil} were measured with psychrometers installed in soil layers at the same depth where the root was found. The line is an exponential function fitted to the data ($y = 0.41 + 1.41 \times (1 - \exp(-3.38x))$, $P < 0.0001$). All species for which root water potential data were available for different times during the dry season are shown.

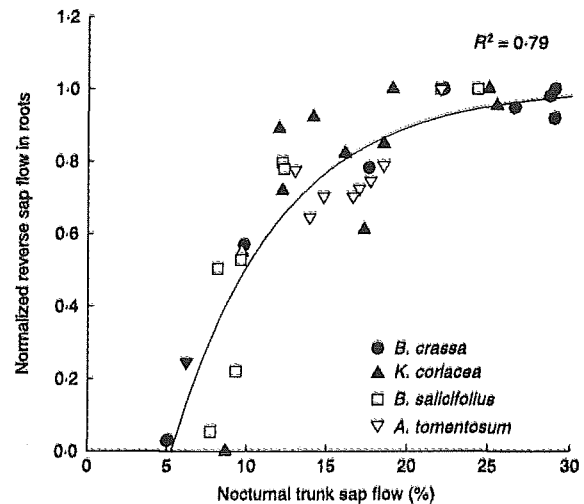


Fig. 7. Normalized total daily reverse sap flow in roots of four Cerrado woody species during the dry season as a function of total daily nocturnal sap flow measured at the base of the main stem or trunk. Nocturnal sap flow was expressed as a percentage with respect to total daily water use per plant. The line represents an exponential function fitted to the data ($y = -1.2 + 3 \times 10^{-5}(1 - \exp(-2 \times 10^{-5}x)) + 2.2(1 - \exp(-0.15x))$, $P < 0.0001$, $n = 39$). All species in which sap flux was measured from the beginning to the end of the dry season of 2003 are shown.

between the lateral roots and the tap root and on the total amount of water loss during the dry season, compared to wet season values. It appears that 'lateral roots' in evergreen species are not really lateral, as they ultimately have a downward rather than sideward tropism. So functionally they appear to be very similar to tap roots. These species with monomorphic root systems might conduct some hydraulic lift through finer diameter roots colonizing upper soil layers. Although we cannot rule out that a few roots of evergreen species may have reverse flow, compared to the abundance of small as well as relatively large roots of deciduous and brevideciduous species, the amount of water released by shallow roots in evergreen trees should be negligible.

Regardless of some differences in vertical partitioning of water uptake during the dry season, species from all three phenological groups were capable of utilizing relatively deep soil water. Our findings concerning reliance on deep water sources by both deciduous and evergreen species during the dry season are consistent with soil water depletion studies in the Cerrado using time-domain reflectrometry (Oliveira *et al.* 2005a) and neutron probes (Quesada *et al.* 2004) showing that soil compartments below 100 cm contribute about 80% of the total water used during dry season.

DETERMINANTS OF REVERSE FLOW IN LATERAL ROOTS

Several studies have found that hydraulic redistribution at the stand level is triggered when Ψ in the upper soil falls below -0.4 to -0.7 MPa (Caldwell & Richards 1989; Dawson 1993;

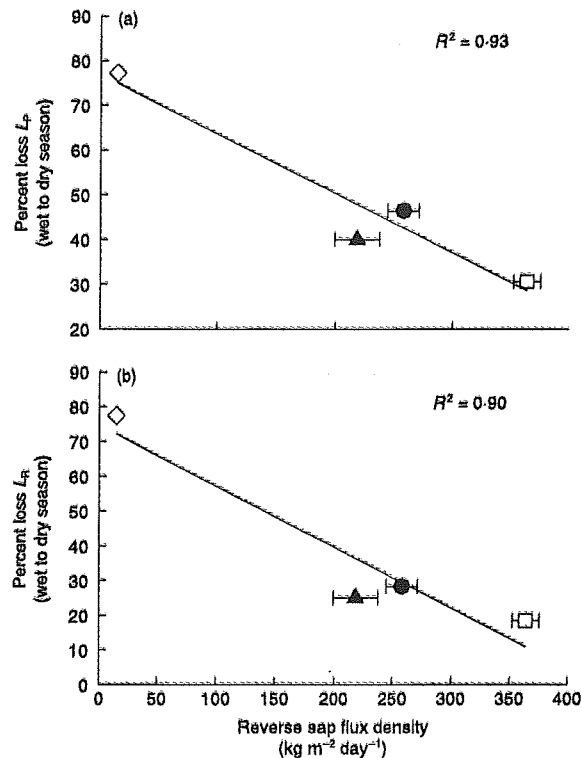


Fig. 8. (a) Percent loss of total root hydraulic conductance (L_p) and (b) percent loss of radial conductance (L_i) from the wet to the dry season in relation to total daily reverse sap flux in lateral roots at the peak of the dry season. Values of reverse sap flux are means ($\pm$ SE) of three to six roots in different trees. Values of L_p and L_i are means of three to six different roots measured during the wet seasons (January 2004) and the dry (August 2004) in different trees. For *K. coriacea* only two roots were obtained during the dry season. A linear regression was fitted to each relationship (a) $y = 77 - 0.13x$, $P = 0.035$; (b) $y = 74.5 - 0.17x$, $P = 0.05$. Symbols are: (o) *B. crassa*, (Δ) *K. coriacea*, ($\square$) *B. salicifolius* and ($>$) *Q. parviflora*.

Millikin Ishikawa & Bledsoe 2000; Meinzer *et al.* 2004; Brooks *et al.* 2006). However, the relevant driving force governing the seasonal dynamics of hydraulic lift is the difference between Ψ_{soil} and Ψ_{root} rather than Ψ_{soil} alone. Reverse sap flow in lateral roots of three of the deciduous and brevidiciduous species studied increased asymptotically with $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$. When $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$ increased beyond 0.8 MPa, the reverse sap flow remained nearly constant despite the increase in the driving force. Multiple factors, including partial loss of root conductivity during the dry season and decreases in soil hydraulic conductivity were likely to have contributed to this behaviour. The percent loss of total hydraulic conductivity (L_p) and radial conductivity (L_i) in shallow lateral roots increased during the dry season. However, the magnitude of the seasonal decline in L_p and L_i was species-specific and depended on rates of reverse sap flow.

Other factors may also partially explain why reverse sap flow in lateral roots became independent of $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$ above 0.8 MPa. Nocturnal transpiration is prevalent in Cerrado woody species during the dry season (Bucci *et al.* 2004; Scholz

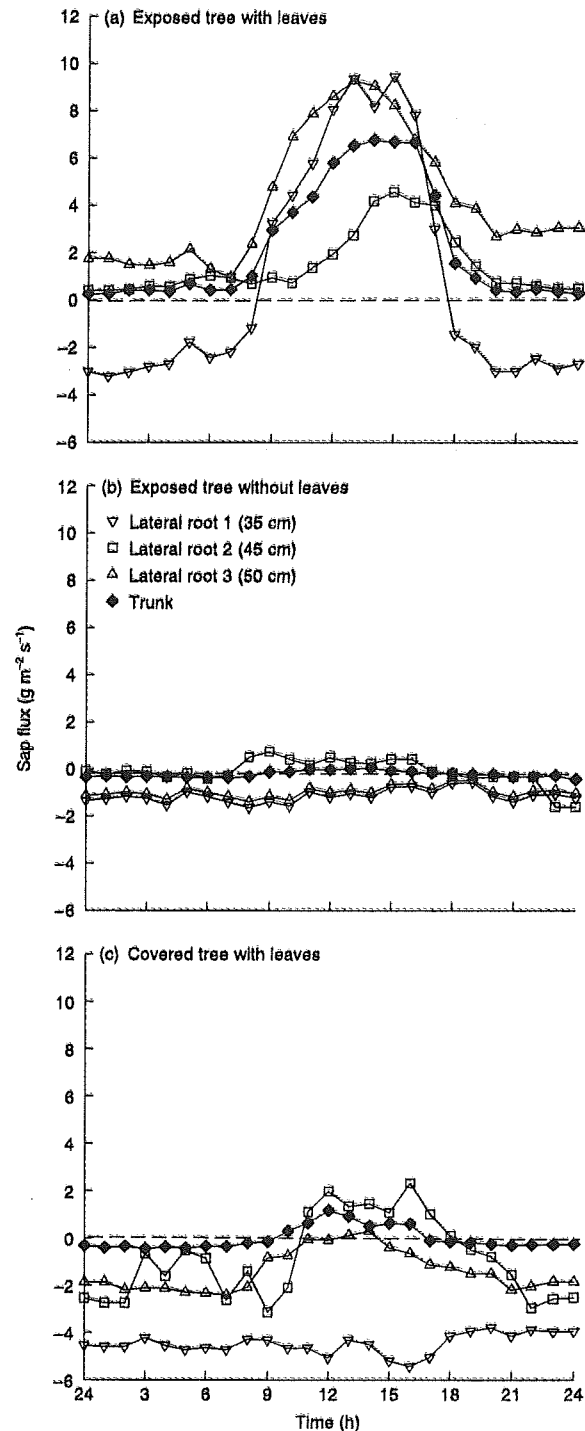


Fig. 9. Time courses of sap flux in roots and the main stem in a *K. coriacea* tree (a) with a full leaf crown during one day in the middle of the dry season (2 July 2003), (b) leafless (4 August 2003), and (c) with the crown covered with opaque bags to reduce transpirational water loss in the middle of the dry season (27 June 2003). Root depths are indicated in panel (b).

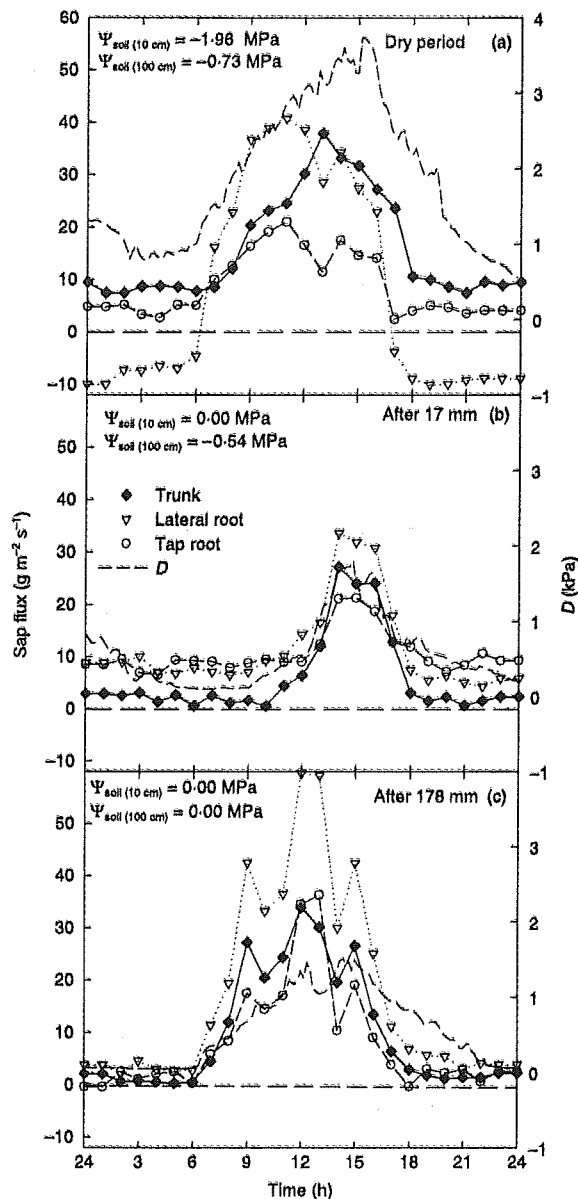


Fig. 10. Diel courses of sap flux in the tap root, lateral roots and the main stem of a *B. crassa* tree (a) before the beginning of the rainy season, on 27 October 2002 (b) after a 17-mm rainfall event on 29 October 2002, and (c) after a heavy 178-mm rainfall event on 9 November 2002. Diel changes in air saturation deficits (D) are included in each panel as well as information on soil water potential (Ψ_{soil}) at 10 and 100 cm below the soil surface.

et al. 2007a) and may represent an additional competing sink for water taken up by deep roots that may otherwise be released by shallow roots to the upper soil layers. Reverse sap flow in lateral roots of deciduous and brevidciduous species increased asymptotically with increasing nocturnal sap flow through the main stem, implying that nocturnal transpiration can limit the magnitude of hydraulic lift. When the competing foliage sink for water was removed, by covering an individual

of *K. coriacea* to prevent nocturnal transpiration, the rate of reverse sap flow in shallow roots increased (Fig. 9c). Similar responses of hydraulic lift to alteration of Ψ driving forces and competing sinks were reported in earlier studies (Scholz *et al.* 2002; Hultine *et al.* 2003; Brooks *et al.* 2006). Moreover, in a recent study of three dominant Cerrado woody species, Scholz *et al.* (2007a) observed that the species exhibiting the most frequent hydraulic lift during the dry season was the one with the lowest nocturnal stomatal conductance. Water storage in stem tissues contributes between 10% and 31% to total daily water loss and is an important determinant of the daily dynamics of water relations in Cerrado trees (Scholz *et al.* 2007b; Scholz *et al.* 2008). Stem water storage tissues that are refilled during the late afternoon and at night when evaporative demand and water loss are low (Bucci *et al.* 2004; Scholz *et al.* 2008) can constitute a competing sink for water taken up by tap or deep roots that could be otherwise released to drier regions in the profile soil by shallow roots. Thus, in the presence of high nocturnal transpiration or recharge of internal water storage, Ψ_{root} could remain below or close to Ψ_{soil} eliminating or limiting reverse sap flow and hydraulic lift. The relative strength of these competing sinks will determine the direction and magnitude of the water sap flow in roots. All these variables (hydraulic lift, night-time transpiration and stem capacitance) can prevent equilibration along the soil to leaf continuum, resulting in a predawn leaf water potential more negative than Ψ_{soil} (Donovan, Linton & Richards 2001; Bucci *et al.* 2004; Bucci *et al.* 2005; Scholz *et al.* 2007b).

DOWNWARD HYDRAULIC REDISTRIBUTION

In some vegetation types, the first rainfall events after a long dry period can result in downward hydraulic redistribution from the upper to lower soil layers through roots (Burgess *et al.* 1998; Smith *et al.* 1999; Burgess *et al.* 2001; Oliveira *et al.* 2005b). However, in the present study none of the five individuals specially fitted with heat pulse sensors during the dry to rainy season transition period exhibited downward sap flow in the tap root (data shown only for *B. crassa*). The following two factors may explain the lack of downward hydraulic redistribution in the Cerrado species studied: (i) the tap root is exploring deep soil layers with abundant water and consequently after the first conspicuous rain event during the dry to wet season transition, the soil water potential gradient between upper soil and deep soil layers becomes small or nonexistent, (ii) Cerrado soils have a very high saturated hydraulic conductivity (about 100 cm h⁻¹ at 10 cm depth and about 6 cm h⁻¹ at 100 cm depth; Scholz 2006) and the infiltration rates are also high (1'26 m h⁻¹, Eiyti2001). Consequently, even in the absence of a shallow to deep root pathway, the soil water potential gradients developed during the dry season can be rapidly eliminated after a large rainfall event at the beginning of the rainy season. Nevertheless, downward hydraulic redistribution may occur in Cerrado trees under certain conditions. In an earlier study, we recorded a few hours of nocturnal reverse flow in a tap root of a Cerrado tree

after a rainfall event that ended a long rainless period (Scholz *et al.* 2002). We believe that downward hydraulic redistribution seldom occurs in Cerrado trees, and when it does, it is a phenomenon of very short duration without an important role in the hydrological cycle of Neotropical savanna ecosystems.

FUNCTIONAL SIGNIFICANCE OF HYDRAULIC LIFT

Results from this study showed that the percent loss of total and radial root hydraulic conductivity in lateral shallow roots between the wet and dry season decreased linearly with increasing reverse sap flow among four deciduous and brevideciduous species. The relative permeability of roots to water tends to vary directly with water availability in the soil (Huang & Nobel 1993). This dependence of root L_p on soil moisture conditions has been referred to as rectifier-like behaviour in roots of desert plants (Nobel & Sanderson 1984), and was associated with physiological and anatomical changes that led to large decreases in axial and radial hydraulic conductivity (North & Nobel 1996). In the present study, hydraulic lift and the associated reverse sap flow in lateral roots were sufficient to maintain root hydraulic conductivity at a level that prevented complete root rectification. Similarly, Domec *et al.* (2004) found that partial overnight replenishment of soil water by hydraulic lift in old-growth ponderosa pine and Douglas-fir stands prevented Ψ_{soil} from falling to levels that would have induced complete loss of water transport capacity in shallow roots compared to stands with young trees where the magnitude of hydraulic lift was low. In a recent study, Bauerle *et al.* (2008), showed that *grapevines*, a species capable of hydraulic lift (Smart *et al.* 2005), have roots with similar life spans in both the wet and dry seasons, suggesting that in this species hydraulic lift could contribute to the avoidance of substantial seasonal reductions in root water potential, thereby prolonging root survivorship in dry soil layers.

In addition to the pronounced seasonality of precipitation, Cerrado soils are old and weathered with low nutrient availability, particularly N and P (Haridasan 2000; Kozovits *et al.* 2007). Consequently, the ability of hydraulic lift to maintain high root hydraulic conductivity in the upper soil layers should facilitate nutrient acquisition during the dry season even if its direct impact on the amount of water taken up is negligible, and could permit rapid responses to rain pulses at the onset of the rainy season. Additionally, hydraulic lift is also likely to influence carbon and nutrient cycling in seasonal ecosystems through its effects on rhizosphere fungi. Querejeta *et al.* (2003, 2007) demonstrated that water hydraulically lifted by *Quercus agrifolia* was distributed to mycorrhizal hyphae, enabling them to maintain their activity in dry soil. Although the estimated amount of hydraulically lifted water released to dry soil by Cerrado trees constituted only about 1% of the total water use at the stand level (Scholz 2006; Bucci *et al.* 2008), it is likely to play an important role in maintaining nutrient uptake and the viability of symbiotic associations, and in preventing complete cavitation of the xylem conduits in upper roots during the dry season (Domec *et al.* 2006; Bauerle *et al.* 2008).

According to the results of our study, deciduous and brevideciduous species were the only ones with a high frequency of lateral roots exploring nutrient rich soil layers. These species also have leaf N and P concentrations that are higher than those of evergreen species and also have relatively short leaf life spans (Franco *et al.* 2005). Evergreen species in Cerrado ecosystems appear to have a nutrient-conserving and water-spending strategy because they allocate much biomass to large deep roots to secure reliable access to deep moisture during the dry season at the cost of poor access to nutrient-rich upper soil layers, thus resulting in low foliar nutrient concentrations and slow leaf turnover. By contrast, deciduous and brevideciduous species with their high foliar nutrient concentrations and relatively short leaf life spans and greater allocation of biomass to roots in nutrient-rich upper soil layers, appear to have a less nutrient-conserving strategy, and more of a water-conserving strategy as they greatly limit transpiration by dropping leaves and reducing stomatal conductance during the dry season (Bucci *et al.* 2005). There appears to be a trade-off between greater year round access to nutrients in the upper soil layers (deciduous and brevideciduous species), and a greater access to deep moisture during the dry season (evergreen species). Species-specific differences in root architecture could thus have important implications for whole-ecosystem water, carbon and nutrient balance. Deciduous and brevideciduous species with dimorphic root systems represent close to 50% of the woody component in Cerrado ecosystems (Lenza & Klink 2006) and consequently may contribute more to nutrient cycling than evergreen species, not only because they exploit upper soil horizons with higher levels of available nutrients, but also because hydraulic lift through the release of water into the rhizosphere could facilitate processes related to mineralization, organic matter decomposition and symbiotic interactions. These predictions may be relevant for other seasonal tropical to sub-tropical ecosystems with similar plant adaptations such as trees growing on karst soil (Querejeta *et al.* 2007) and Acacia-dominated systems (Ludwig *et al.* 2003).

Acknowledgements

This work was supported by grants from the National Science Foundation (USA) grant #0296174 and grant # 0322051 and CNPq Brazil. Special thanks to Gretchen North for help with methods for measuring total and radial root hydraulic conductivity. Authors thank the IBGE Ecological reserve for logistic support and to Jose Hinojosa for providing useful field assistance.

References

- Bauerle, T.L., Richards, J.H., Smart, D.R. & Eissenstat, D.M. (2008) Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant, Cell and Environment*, 31, 177–186.
- Brooks, J.R., Meinzer, F.C., Coulombe, R. & Gregg, I. (2002) Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology*, 22, 1107–1117.
- Brooks, J.R., Meinzer, F.C., Warren, J.M., Domec, J.C. & Coulombe, R. (2006) Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. *Plant, Cell and Environment*, 29, 138–150.
- 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, E.G., Goldstein, G., Meinzer, E.C., Hinojosa, J.A., Hoffmann, W.A. & Franco, A.C. (2004) Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. *Tree Physiology*, 24, 1119-1127.
- Bucci, S.J., Goldstein, G., Meinzer, E.C., Franco, A.C., Campanello, P. & Scholz, E.C. (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plants in Neotropical savanna trees. *Trees*, 19, 296-304.
- Bucci, S.J., Scholz, E.G., Goldstein, G., Hoffmann, W.A., Meinzer, E.C., Franco, A.C., Giambelluca, T. & Miralles-Wilhelm, E. (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.
- Burgess, S.O., Adams, M.A., Turner, N.C., White, D.A. & Ong, C.K. (2001) Tree roots: conduits for deep recharge of soil water. *Oecologia*, 126, 158-165.
- Burgess, S.S.O., Adams, M.A., Turner, N.C. & Ong, C.K. (1998) The redistribution of soil water by tree root systems. *Oecologia*, 115, 306-311.
- Caldwell, M.M. & Richards, J.H. (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by roots. *Oecologia*, 79, 1-5.
- Caldwell, M.M., Dawson, T.E. & Richards, J.H. (1998) Hydraulic lift - consequences of water efflux from the root of plants. *Oecologia*, 113, 151-161.
- Castro, L.H.R. & Kauffman, J. (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.
- Cochrane, T.T. (1989) Chemical properties of native savanna and forest soils in central Brazil. *Soil Science Society of America Journal*, 53, 139-141.
- Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, 95, 565-574.
- Domec, J.C., Warren, J.M., Meinzer, E.C., Brooks, J.R. & Coulombe, R. (2004) Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia*, 141, 7-16.
- Domec, J.C., Scholz, E.G., Bucci, S.J., Meinzer, E.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.
- Donovan, L.A., Linton, M.J. & Richards, J.H. (2001) Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. *Oecologia*, 129, 328-335.
- Eiyti, K. (2001) *Efeito da Queimada na Estabilidade de Agregados da Resiliência ao Seloamento Superficial e na Taxa de Infiltração de Água em Solos de Cerrado*. PhD thesis, University of Brasília, Brazil.
- Felfili, J.M., Haridasan, M., Cunha de Mendoza, R., Filgueiras, T., Silva, M.E. & Rezende, A.V. (1994) Projeto biogeografia do bioma Cerrado: vegetação e solos. *Cadernos de Geociências (Rio de Janeiro)*, October-December, 75-166.
- Felfili, J.M., Silva Junior, M.C., Filgueiras, T.C. & Nogueira, P.E. (1998) A comparative study of cerrado (sensu stricto) vegetation in Central Brazil. *Ciencia Cultura (Sao Paulo)*, 50, 237-243.
- Franco, A.C. (1998) Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen savanna species. *Plant Ecology*, 136, 69-76.
- Franco, A.C., Bustamante, M., Caldas, L.S., Goldstein, G., Meinzer, E.C., Kozovits, A.R., Rundel, P. & Coradin, V. (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees*, 19, 326-335.
- Goldstein, G., Sarmiento, G. & Meinzer, F.C. (1985) Patrones diarios y estacionales en las relaciones hídricas de árboles siempreverdes de la sabana tropical. *Oecologia Plantarum*, 7, 107-119.
- Goodland, R. (1971) A physiognomic analysis of 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.
- Hill, T.L. (1969) *The Savanna Landscapes of the Amazon Basin*. Savannas Research Series No. 14. Department Of Geography, McGill University, Montreal, Canada.
- HolTmann, W.A., da Silva, E.R., Machado, G.C., Bucci, S.J., Scholz, E.G., Goldstein, G. & Meinzer, E.C. (2005) Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. *Oecologia*, 145, 307-316.
- Huang, B. & Nobel, P.S. (1993) Hydraulic conductivity and anatomy for lateral roots of cacti: changes with soil water availability. *New Phytologist*, 123, 499-507.
- Hultine, K.R., Williams, D.G., Burgess, S.S.O. & Keefer, T.O. (2003) Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia*, 135, 167-175.
- Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.W., Caldas, L., Igle, E. & Causin, F. (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology*, 19, 717-724.
- Kozovits, A.R., Bustamante, M.M.E., Garofalo, C.R., Bucci, S.J., Franco, A.C., Goldstein, G. & Meinzer, F.C. (2007) Responses of plant-soil nutrient dynamics to increased nutrient availability in a central Brazilian savanna. *Functional Ecology*, 21, 1034-1043.
- Landsberg, J. & Fowkes, N.D. (1978) Water movement through plant roots. *Annals of Botany*, 42, 493-508.
- Lenza, E. & Klink, C.A. (2006) Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, OF. *Revista Brasileira de Botânica*, 29, 627-638.
- Ludwig, E., Dawson, T.E., Kroon, H., Berendse, E. & Prins, H.H.T. (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia*, 134, 293-300.
- Medina, E. (1982) Physiological ecology of Neotropical savanna plants. *Ecology of Tropical Savannas* (eds B.J. Huntley & B.H. Walker), pp. 308-335. Springer Berlin Heidelberg, New York.
- Meinzer, E.C., Goldstein, G., Franco, A.C., Bustamante, M., Igle, E., Jackson, P., Caldas, L. & Rundel, P.W. (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian Cerrado woody species. *Functional Ecology*, 13, 273-282.
- Meinzer, E.C., Brooks, J.R., Bucci, S.J., Goldstein, G., Scholz, E.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.
- Millikin Ishikawa, C. & Bledsoe, C.S. (2000) Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: evidence for hydraulic lift. *Oecologia*, 125, 459-465.
- Moreira, M.Z., Sternberg, L.S.L. & Nepstad, D.C. (2000) Vertical patterns of soil water uptake by plants in a primary forest and an abandoned pasture in the eastern Amazon: an isotopic approach. *Plant and Soil*, 222, 95-107.
- Moreira, M.Z., Scholz, E.G., Bucci, S.J., Sternberg, L.S., Goldstein, G., Meinzer, E.C. & Franco, A.C. (2003) Hydraulic lift in a Neotropical savanna. *Functional Ecology*, 17, 573-581.
- Nobel, P.S. & Sanderson, J. (1984) Rectifier-like 'activities' of roots of two desert succulents. *Journal of Experimental Botany*, 35, 727-737.
- Nobel, P.S., Schulte, P.J. & North, G.B. (1990) Water influx characteristics and hydraulic conductivity for roots of *Agave deserti* Engelm. *Journal of Experimental Botany*, 41, 409-415.
- North, G.B. & Nobel, P.S. (1996) Radial hydraulic conductivity of individual root tissues of *Opuntia ficus-indica* (L.) Miller as soil moisture varies. *Annals of Botany*, 77, 133-142.
- Oliveira, R.S., Beserra, L., Davidson, B.A., Pinto, F., Klink, C.A., Nepstad, D.C. & Moreira, A. (2005a) Deep root function in soil water dynamics in cerrado savanna of central Brazil. *Functional Ecology*, 19, 574-581.
- Oliveira, R.S., Dawson, T.E., Burgess, S.O. & Nepstad, D.C. (2005b) Hydraulic redistribution in three Amazonian trees. *Oecologia*, 145, 354-363.
- Oliveira-Filho, A.T., Vilela, E.A., Carvalho, D.A. & Gavilanes, M.L. (1994) Effects of soils and topography on the distribution of tree species in a tropical riverine forest in south-eastern Brazil. *Journal of Tropical Ecology*, 10, 483-508.
- Plamboeck, A.H., Dawson, T.E., Egerton-Warburton, L.M., North, M., Bruns, T.O. & Querejeta, J.L. (2007) Water transfer via ectomycorrhizal fungal hyphae to conifer seedlings. *Mycorrhiza*, 17, 439-447.
- Querejeta, J.L., Egerton-Warburton, L.M. & Allen, M.E. (2003) Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia*, 134, 55-64.
- Querejeta, J.L., Egerton-Warburton, L.M. & Allen, M.E. (2007) Hydraulic lift may buffer rhizosphere biophysics against the negative effects of severe soil drying in a California Oak savanna. *Soil Biology and Biochemistry*, 29, 409-417.
- Quesada, C.A., Miranda, A.C., Hodnett, M.G., Santos, A.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.B., Andrade, S., Miranda, H.S., Miranda, E. & Lloyd, J. (2008) Seasonal variations in soil water in two woodland savannas of central Brazil with different fire history. *Tree Physiology*, 28, 405-415.
- Ratter, J.A., Bridgewater, S., Atkinson, R. & Ribeiro, J.F. (1996) Analysis of the floristic composition of the Brazilian cerrado vegetation II: comparison of the woody vegetation of 98 areas. *Journal of Botany*, 53, 153-180.
- Rawitscher, E. (1948) The water economy of vegetation of the campos cerrados in Southern Brazil. *Journal of Ecology*, 36, 238-168.
- Richards, J.H. & Caldwell, M.M. (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 73, 486-489.
- Sarmiento, G. (1984) *The Ecology of Neotropical Savannas*. Harvard University Press, Cambridge.

- Sarmiento, G., Goldstein, G. & Meinzer, FC. (1985) Adaptative strategies of woody species in Neotropical savannas. *Biology Review*, 60, 315-355.
- Scholz, FG. (2006) *Biofísica del Transporte de agua en el Sistema Suelo-planta: Redistribución, Resistencia y Capacitancias Hidráulicas*. PhD thesis, University of Buenos Aires, Argentina.
- Scholz, FG., Bucci, S.J., Goldstein, G., Meinzer, FC. & Franco, A.C. (2002) Hydraulic redistribution of soil water by Neotropical savanna trees. *Tree Physiology*, 22, 603-612.
- Scholz, FG., Bucci, S.J., Goldstein, G., Meinzer, FC., Franco, A.C. & Miralles-Wilhelm, F (2007a) Removal of nutrient limitations by long-term fertilization decreases nocturnal water loss in savanna trees. *Tree Physiology*, 27, 551-559.
- Scholz, FG., Bucci, S.J., Goldstein, G., Meinzer, FC., Franco, A.C. & Miralles-Wilhelm, F (2007b) Biophysical properties and functional significance of stem water storage tissues in nee-tropical savanna trees. *Plant, Cell and Environment*, 30, 236-248.
- Scholz, FG., Bucci, S.J., Goldstein, G., Meinzer, FC., Franco, A.C., Miralles-Wilhelm, F (2008) Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. *Tree Physiology*, 28, 469-480.
- Simmoneau, T. & Habib, R. (1991) The use of tree root suckers to estimate the root water potential. *Plant Cell and Environment*, 14, 585-591.
- Smart, D.R., Carlisle, E., Goebel, M. & Nunez, B.A. (2005) Transverse hydraulic redistribution by a grapevine. *Plant Cell and Environment*, 28, 157-166.
- Smith, D.M., Jackson, N.A., Roberts, J.M. & Ong, C.K. (1999) Reverse flow of sap in tree roots and downward siphoning of water by *Grevillea robusta*. *Functional Ecology*, 13, 256-264.
- Warren, J.M., Brooks, J.R., Meinzer, F. & Eberhart, J.L. (2008) Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. *New Phytologist*, 178, 382-394.

Received 17 March 2008; accepted 16 June 2008

Handling Editor: Matthew Turnbull