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

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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

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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 ($\Psi$) 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 might facilitate or impede the occurrence of 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 neighboring 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 (Hofmann 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 fulfill the requirements for hydraulic lift to occur (e.g. Scholz et al. 2002; Moreira et al. 2003; Meinder 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 experimetal 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, savannaphysiognomies with intermediated density cerrado denso savanna with basal area of 18.2 m² ha⁻¹ and campo cerrado, an open tree and shrub savanna with basal area of 4.4 m² 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 Brasilia (15° 56'S, 47° 53'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...
Tree height and basal diameter are expressed as mean ± SE (n = 3 to 15).

<table>
<thead>
<tr>
<th>Species</th>
<th>Leaf phenology</th>
<th>Height (m)</th>
<th>Basal diameter (cm)</th>
<th>Number of trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schefflera macrocarpa</td>
<td>Evergreen</td>
<td>3.9 ± 0.2</td>
<td>11.2 ± 0.9</td>
<td>6</td>
</tr>
<tr>
<td>Sclerolobium paniculatum</td>
<td>Evergreen</td>
<td>6.0 ± 0.3</td>
<td>15.3 ± 1.1</td>
<td>4</td>
</tr>
<tr>
<td>Vochysia elliptica</td>
<td>Evergreen</td>
<td>4.0 ± 0.2</td>
<td>5.1 ± 0.1</td>
<td>5</td>
</tr>
<tr>
<td>Byrsonima crassus</td>
<td>Brevideciduous</td>
<td>2.1 ± 0.1</td>
<td>9.0 ± 0.4</td>
<td>35</td>
</tr>
<tr>
<td>Blepharocalyx salicifolius</td>
<td>Brevideciduous</td>
<td>4.0 ± 0.1</td>
<td>9.6 ± 0.6</td>
<td>35</td>
</tr>
<tr>
<td>Dalbergia miticobolium</td>
<td>Brevideciduous</td>
<td>4.2 ± 0.3</td>
<td>12.6 ± 1.3</td>
<td>5</td>
</tr>
<tr>
<td>Aspidosperma tomentosum</td>
<td>Deciduous</td>
<td>3.2 ± 0.3</td>
<td>4.4 ± 0.3</td>
<td>5</td>
</tr>
<tr>
<td>Kielmeyera coriacea</td>
<td>Deciduous</td>
<td>2.6 ± 0.2</td>
<td>5.6 ± 0.5</td>
<td>35</td>
</tr>
<tr>
<td>Quatea parviflora</td>
<td>Deciduous</td>
<td>2.6 ± 0.2</td>
<td>5.2 ± 0.3</td>
<td>25</td>
</tr>
</tbody>
</table>
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 (Ψsat) 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 Ψsat at 100 cm depth decreased in a nearly continuous manner.

Diel patterns of root and stem sap flux (gm⁻²s⁻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 -52 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 brevideciduous 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 laterals roots decreased toward the end of the dry season in the deciduous and brevideciduous 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 brevideciduous 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.
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 $\Psi_{\text{soil}}$ to $\Psi_{\text{root}}$ 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 remained constant, the percent loss of total and radial hydraulic conductivity ($L_R$) 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 $K$. 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 (cm$^3$ 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.

<table>
<thead>
<tr>
<th>Sap flow (cm$^3$ day$^{-1}$)</th>
<th>Wet season</th>
<th>Early dry season</th>
<th>Dry season</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>K. coriacea deciduous</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trunk</td>
<td>1140</td>
<td>577</td>
<td>149</td>
</tr>
<tr>
<td>Lateral root</td>
<td>264 (23%)</td>
<td>3-8 (0-7%)</td>
<td>3-8 (2-5%)</td>
</tr>
<tr>
<td>Tap root</td>
<td>156 (13%)</td>
<td>273 (47%)</td>
<td>70 (47%)</td>
</tr>
<tr>
<td><strong>B. crassa brevideciduous</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trunk</td>
<td>553</td>
<td>336</td>
<td>128</td>
</tr>
<tr>
<td>Lateral root</td>
<td>27 (4-9%)</td>
<td>8-8 (2-6%)</td>
<td>-13.5 (4%)</td>
</tr>
<tr>
<td>Tap root</td>
<td>166 (30%)</td>
<td>124 (37%)</td>
<td>75 (38-6%)</td>
</tr>
<tr>
<td><strong>S. macrocarpa evergreen</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trunk</td>
<td>1286</td>
<td>1192</td>
<td>1243</td>
</tr>
<tr>
<td>Lateral root</td>
<td>486 (37-8%)</td>
<td>407 (34-1%)</td>
<td>419 (33-8%)</td>
</tr>
<tr>
<td>Tap root</td>
<td>237 (18-4%)</td>
<td>207 (17-4%)</td>
<td>200 (16-1%)</td>
</tr>
</tbody>
</table>
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 brevideciduous 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 brevideciduous 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.
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Fig. 5. (a) Log of difference between the hydrogen isotope ratio ($\delta D$) of water obtained from lateral roots of the treated plants (tap root supplied with deuterated water) and $\delta D$ of root water ($\delta D_{\text{root}}$) from the control plants whose tap roots were not supplied with deuterated water, and (b) Log of difference between $\delta D$ of soil water around the roots of the treated plants and $\delta D$ of soil water around roots of control plants ($\delta D_{\text{soil}}$). Actual $\delta D$ values equivalent to those indicated on the log scale are shown on the right axis. Soil and root water with $\delta D$ 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 $P < 0.01$. The species studied were: Qp: Qualea parviflora (Q, Bs: Blepharocalyx sallcifolius (]), Be: Byrsonima crassa (o), Kc: Kielmeyera coriacea (A) and At: Aspidosperma tomentosum (T).

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 ($\Psi_{\text{soil}} - \Psi_{\text{root}}$) 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 $\Psi_{\text{root}}$ 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 ($y = -0.41 + 1.41 \times (\exp(-3.38x)), R^2 = 0.87$). 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 ($y = -1.2 + 3 \times 10^5 (1 - \exp(-2 \times 10^{-5x})) + 2(1 - \exp(-0.15x)), R^2 = 0.79$, $P < 0.0001$, $n = 39$). All species in which sap flux was measured from the beginning to the end of the dry season of 2003 are shown.

DETERMINANTS OF REVERSE FLOW IN LATERAL ROOTS

Several studies have found that hydraulic redistribution at the stand level is triggered when $\Psi$ in the upper soil falls below -0.4 to -0.7 MPa (Caldwell & Rickards 1989; Dawson 1993;
Fig. 8. (a) Percent loss of total root hydraulic conductance ($L_p$) and (b) percent loss of radial conductance ($L_R$) 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 (± SE) of three to six roots in different trees. Values of $L_p$ and $L_R$ 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: (○) *B. crassa*, (Δ) *K. coriacea*, ([)] *B. salicifolius* and (<>*) *Q. parviflora*.

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).
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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<sub>root</sub> could remain below or close to Ψ<sub>soil</sub> 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<sub>soil</sub> (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 wet 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<sup>-1</sup> at 10 cm depth and about 6 cm h<sup>-1</sup> at 100 cm depth; Scholz 2006) and the infiltration rates are also high (1'26 m h<sup>-1</sup>, Eiyiti2001). 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 behavior 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 $\Psi_{soil}$ 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).

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References


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