



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

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

# 1 **Biophysical and life history determinants of hydraulic lift in**

## 2 **Neotropical savanna trees**

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23 Running headline: Hydraulic lift in Neotropical savannas

## 1 SUMMARY

- 2 1. Measurements of sap flow in taproots, lateral roots and stems, as well as stable  
3 isotope labeling techniques were used to determine the occurrence and relative  
4 magnitude of hydraulic lift in several individuals of nine co-occurring Brazilian  
5 savanna (Cerrado) tree species and to assess physical and biological determinants of  
6 this process at tree and ecosystem level.
- 7 2. The occurrence of reverse sap flow observed in deciduous and brevideciduous species  
8 during the dry season was consistent with hydraulic lift. Maximum reverse sap flux in  
9 lateral roots was  $5.2 \text{ g m}^{-2} \text{ s}^{-1}$  for deciduous species and  $16.3 \text{ g m}^{-2} \text{ s}^{-1}$  for  
10 brevideciduous species. The evergreen species did not exhibit reverse flow in lateral  
11 roots. Consistent with their ability to carry out hydraulic lift, the brevideciduous and  
12 deciduous species had dimorphic root systems, whereas the evergreen species had  
13 monomorphic root systems.
- 14 3. In the deciduous and brevideciduous species, the contribution of tap roots to  
15 transpiration increased substantially as the dry season progressed. Seasonal changes  
16 in the contribution of tap roots to transpiration were not evident in the evergreen  
17 species.
- 18 4. There was an inverse relationship between rates of reverse sap flow and seasonal loss  
19 of hydraulic conductivity in lateral roots, suggesting that hydraulic lift in Cerrado  
20 woody plants may help maintain the functionality of the lateral roots in exploring dry  
21 and nutrient rich superficial soil layers without directly enhancing the amount of  
22 water uptake.

- 1 5. Reverse sap flow in lateral roots of the deciduous and brevideciduous species  
2 increased asymptotically as the driving force for water movement from roots to the  
3 soil increased. The non-linear relationship between reverse sap flow and its driving  
4 force implied that additional sinks for water such as nocturnal transpiration and  
5 refilling of internal water storage tissues may compete for internal water resources  
6 during the dry season.
- 7 6. Downward hydraulic redistribution from upper to deeper soil layers through tap roots  
8 at the beginning of the wet season seldom occurred in Cerrado trees, and when it did  
9 it was a phenomenon of very short duration without an important role in the  
10 hydrological cycle.

11

12 *Key-words:* Hydraulic redistribution; leaf phenology; nocturnal transpiration; root  
13 architecture; root conductivity.

## 1 INTRODUCTION

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

17 It is believed that hydraulic lift can contribute significantly both to the water balance  
18 of the plants responsible for it and that of neighboring plants of the same or other species  
19 (Dawson 1993; Moreira *et al.* 2003). Water released from roots into drier soil layers may be-  
20 re-absorbed when transpiration exceeds water uptake by deep roots alone (Richards &  
21 Caldwell 1987). In addition to improving plant water balance during periods with low  
22 precipitation, hydraulic lift may also enhance nutrient uptake by fine roots located in the  
23 relatively nutrient rich portion of the soil profile, which normally undergoes desiccation in

1 environments characterized by a pronounced dry season (Caldwell, Dawson & Richards  
2 1998), and may help to maintain the activity of mycorrhizae and symbiotic nitrogen fixing  
3 bacteria as the bulk soil in the upper portion of the profile dries (Querejeta, Egerton-  
4 Warburton & Allen 2003; Querejeta, Egerton-Warburton & Allen 2007; Plamboeck *et al.*  
5 2007).

6 Tropical savannas are the second most extensive vegetation type in South America,  
7 and among them, the Cerrado of central Brazil forms the largest regional system (Goodland  
8 1971). Cerrado communities are characterized by high tree species diversity (Sarmiento  
9 1984). More than 500 species of trees and large shrubs are present within savanna  
10 ecosystems in the Cerrado region (Ratter *et al.* 1996), and even relatively small areas may  
11 contain up to 70 or more species of vascular plants (Felfili *et al.* 1998). The principal factors  
12 influencing the structure of Cerrado vegetation include not only a pronounced seasonality of  
13 precipitation, frequent fires and low soil fertility (Haridasan 2000), but also high  
14 temperatures and low humidity (e.g. Hill 1969; Medina 1982; Cochrane 1989). The low  
15 relative humidity and relatively high daytime temperatures in the Cerrado impose a  
16 consistently high evaporative demand during the prolonged dry season. During this period,  
17 water in the upper soil layers is severely depleted as evidenced by the dieback of grasses  
18 (Hoffmann *et al.* 2005) and by the low water potential (more negative) in the upper portion  
19 of the soil profile (Franco 1998), while deeper layers retain high water content even after  
20 several months without rain (Quesada *et al.* 2004, 2008). These environmental conditions  
21 fulfill the requirements for hydraulic lift to occur (e.g. Scholz *et al.* 2002; Moreira *et al.*  
22 2003; Meinzer *et al.* 2004).

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

13           Nine dominant evergreen, brevideciduous, and deciduous woody species were  
14 selected for this study. Our objectives were to (1) determine the influence of leaf phenology  
15 and root system architecture on the occurrence of hydraulic lift among Cerrado woody  
16 species, (2) assess other biophysical factors governing hydraulic lift in Cerrado tree species,  
17 and (3) determine potential ecosystem level effects of hydraulic lift in Cerrado vegetation  
18 types. To attain our objectives, we measured stem and root sap flux in several trees using  
19 heat pulse techniques, leaf, root and soil water potentials, air saturation deficits, and  
20 hydraulic conductivities (total, radial and axial) of shallow roots. In addition we performed  
21 experimental manipulations such as feeding of deuterated water to tap roots and covering the  
22 crown of a tree to prevent transpiration.

23

## 1 MATERIALS AND METHODS

### 2 *Site description and plant material*

3 Cerrado vegetation comprises five physiognomic types ranging from *cerradao*, woodland  
4 with a closed or semi-closed canopy, to *campo sujo*, an open savanna with scattered trees and  
5 shrubs. Three savanna physiognomies with intermediate tree density include *cerrado denso*,  
6 *cerrado sensu-stricto* and *campo cerrado*. Cerrado vegetation contains different  
7 combinations of these savanna types organized spatially along gradients of decreasing  
8 abundance of woody plants from *cerradao* to *campo sujo* over distances of only a few km.  
9 The present study was conducted in a *cerrado denso* and a *campo cerrado* stand at the  
10 Instituto Brasileiro de Geografia e Estatística (IBGE) research station located 33 km south  
11 of Brasilia (15° 56'S, 47° 53'W, altitude 1100 m) between August 2000 and January 2004.  
12 Average annual precipitation is about 1500 mm with a pronounced dry season from May to  
13 September. The months of June, July and August are often devoid of precipitation. Mean  
14 monthly temperature ranges from 19 to 23 °C, and diurnal temperature fluctuations of 20 °C  
15 are common during the dry season. The soils are well drained deep oxisols.

16         Nine species among the 25 woody species with the highest measured importance  
17 value indices (Felfili *et al.* 1994) were selected for the study. *Sclerolobium paniculatum* Vog.  
18 (Leguminosae) is an evergreen tree up to 10-m-tall with compound pinnate leaves,  
19 containing four to six large leaflets, *Schefflera macrocarpa* (Seem.) D.C. Frodin (Araliaceae)  
20 is an evergreen tree up to 10-m-tall with palmately compound leaves on branches clustered  
21 near the apex of the stem, *Vochysia elliptica* Mart. (Vochysiaceae) is an evergreen tree  
22 species up to 7-m-tall with simple leaves and short petioles, *Byrsonima crassa* Nied.  
23 (Malpighiaceae) is a brevidecidous shrub or tree up to 5-m-tall with large scleromorphic



1 simple leaves, *Blepharocalyx salicifolius* (H.B. & K.) Berg. (Myrtaceae) is a brevideciduous  
2 tree up to 10-m-tall with small simple leaves, *Dalbergia miscolobium* Benth. (Leguminosae)  
3 is a brevideciduous tree up to 12-m-tall with compound leaves and 5 to 10 pairs of small  
4 leaflets; *Qualea parviflora* Mart. (Vochysiaceae) is a deciduous small tree with simple  
5 opposite leaves; *Kielmeyera coriacea* (Spr) (Clusiaceae). Mart. is a deciduous tree with  
6 simple alternate leaves and short petioles; and *Aspidosperma tomentosum* Mart.  
7 (Apocynaceae) is a deciduous tree up to 15-m-tall with large scleromorphic simple leaves.

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

#### 12 *Environmental variables and soil and root water potential*

13 Relative humidity and air temperature were monitored continuously with probes (HMP35C,  
14 Campbell Scientific, Logan, UT) placed at 12 m and 4 m in height for *cerrado denso* and  
15 *campo cerrado*, respectively, near the center of the study sites. Data were obtained every 10  
16 s, and averaged every 10 minutes averages were recorded with a datalogger (CR10X,  
17 Campbell Scientific, Logan, UT). Air saturation deficit ( $D$ ) was calculated as the difference  
18 between saturation vapor pressure at the air temperature and ambient vapor pressure.

19       Soil psychrometers (PST-55, Wescor, Logan, UT) were used to continuously monitor  
20  $\Psi_{\text{soil}}$  at 10, 20, 30, 60 and 100 cm depth. Before placement in the field, the psychrometers  
21 were individually calibrated against salt solutions of known osmolality following the  
22 procedures of Brown and Bartos (1982). Soil water potential was measured every 30 min  
23 with a 30-s cooling time and data were recorded with a datalogger (CR-7, Campbell

1 Scientific) and corrected for potential temperature gradients according to Brown & Bartos  
2 (1982).

3 Leaf water potential was measured with a pressure chamber (PMS, Albany OR,  
4 USA). Leaf samples were immediately sealed in plastic bags upon excision and kept in a  
5 cooler until balancing pressures were determined in the laboratory within 1 h of sampling  
6 collection. Covered leaf water potential was measured on leaves enclosed in plastic bags and  
7 wrapped in aluminum foil at dusk prior to the measurement day to prevent nocturnal water  
8 loss. Covered leaves make it possible for the water potential in the leaf xylem to be in  
9 equilibrium with that of stem xylem at the point of attachment of the petiole (Simonneau &  
10 Habib 1991). Measurements of water potential were done in three to five leaves per tree  
11 ( $n=3$ ) at dawn. Root water potential ( $\Psi_{\text{root}}$ ) was estimated from the  $\Psi$  of covered leaves  
12 (Domec et al. 2006).

### 13 *Sap flow measurements*

14 Sap flow was measured using a modified heat pulse technique on the excavated central  
15 taproot, on one or more lateral roots, and on the trunk base (Burgess *et al.* 1998; Scholz *et al.*  
16 2002). On some trees we installed heat pulse systems on all the major roots to quantify water  
17 uptake from different layers of the soil profile during the different seasons. Lateral and  
18 taproots were exposed by manually excavating a pit with a radius of approximately 0.75 m  
19 centered on the main trunk. Extreme care was taken to avoid damaging the roots. Heat pulse  
20 probes were installed on tap roots and on lateral roots approximately 10 to 30 cm from the  
21 main trunk. The root region where the probes were installed was covered with soil to  
22 decrease daily temperature fluctuations. When negative flows were observed, zero flow  
23 offset values were determined at the end of the measurement period by severing the proximal

1 and distal ends of a root section containing probes, thereby isolating it from the rest of the  
2 plant (Scholz *et al.* 2002). Calculations pertaining to the heat pulse method are described in  
3 Burgess *et al.* (1998) and Scholz *et al.* (2002).

#### 4 *Deuterium labeling and isotope analysis*

5 Taproots of the plants with heat pulse systems were cut one or two days after the heat pulse  
6 probes were installed. The first cut was approximately at 0.75 m below the root crown.  
7 Taproots were re-cut under water 0.25 m above the first cut to avoid air entry that would  
8 induce embolism. The taproots were fed with 75% D<sub>2</sub>O solutions in calibrated containers that  
9 permitted total volumetric uptake to be recorded. Samples of roots and soil around the roots  
10 were taken 8 days after feeding deuterated water to the tap root and upon termination of sap  
11 flow measurements. Samples were obtained in the morning and sealed in Vacutainer tubes  
12 (7 ml, Becton Dickinson, NJ, USA) for water extraction with vacuum distillation and isotopic  
13 analyses. Soil and lateral root samples of control plants were collected.  
14 Samples were taken to the laboratory for water extraction and analysis of their deuterium  
15 content by mass spectrometry according to Moreira, Sternberg & Nepstad (2000). Hydrogen  
16 isotope ratios ( $\delta D$ ) are expressed as deviation in parts per thousand from the international  
17 standard V-SMOW (Vienna-Standard Mean Ocean Water).

18 A mass balance equation was used to determine the proportion of deuterated water (x)  
19 taken up by the roots of labeled plants.  $\delta D$  values were converted to mole fraction values  
20 and the proportion of label uptake calculated according to the following equation:

$$x = \frac{M_S - M_C}{M_L - M_C};$$

1 where  $M_S$ ,  $M_C$  and  $M_L$  are the mole fractions of deuterium in the stem sample, in the control  
2 stems and in the labeling solution respectively.

### 3 *Root hydraulic conductivity*

4 Total hydraulic conductivity ( $L_P$ ), radial hydraulic conductivity ( $L_R$ ) and axial hydraulic  
5 conductivity ( $K_H$ ) were measured in roots collected between 0530 and 0700 h in January  
6 2004 and August 2004. Four species with different magnitudes of reverse sap flow were  
7 selected for measurements of root conductivity (*B. crassa*, *B. salicifolius*, *K. coriacea* and *Q.*  
8 *parviflora*). Root segments approximately 25-cm-long and 2 to 4 mm in diameter were  
9 excised and immersed in distilled water. In the laboratory, a 15-cm-long section of each root  
10 was re-cut under water, and the bark and cambium were removed from a 1 cm region at the  
11 proximal end. The exposed portion was inserted into 5-mm Tygon tubing attached to a glass  
12 capillary half filled with distilled water. The Tygon tubing was sealed firmly to the outer  
13 sapwood by tightening a compression fitting. The distal cuts ends were sealed with  
14 cyanoacrylate adhesive. Water flow through the roots was induced by applying a partial  
15 vacuum (-10 to -50 kPa) to the open end of the attached capillary while the root segments  
16 were immersed under distilled water. The pressure was adjusted by a needle valve and  
17 monitored using a digital manometer (Cole-Parmer® 68603, USA). A pipette capable of  
18 resolving 0.01-mm<sup>3</sup> and a magnifying glass were used to observe the location of the  
19 meniscus, and the distance traveled by the meniscus along the capillary per unit time was  
20 used to calculate the volumetric flow rate ( $Q_V$ , m<sup>3</sup> s<sup>-1</sup>). When  $Q_V$  became constant at a given  
21 pressure ( $P$ , MPa), root hydraulic conductivity,  $L_P$  (m s<sup>-1</sup> MPa<sup>-1</sup>) was calculated as:

$$22 \quad L_p = (\Delta Q_V / \Delta P)(1/A)$$

1 where  $A$  ( $\text{m}^2$ ) is the lateral surface area of the root segment (Nobel, Schulte & North 1990).  
2 Radial conductance was equated to the volumetric flux density of water ( $\text{m s}^{-1}$ ) at the root  
3 surface divided by the difference in water potential (MPa) from the root surface to the root  
4 xylem. Root radial hydraulic conductivity average over the root segment ( $L_R$ ,  $\text{m s}^{-1} \text{MPa}^{-1}$ )  
5 was calculated as:

$$6 \quad L_R = L_p \alpha / \tanh(\alpha L)$$

7 where  $\alpha$  ( $\text{m}^{-1}$ ) is  $(2 \pi r_{root} L_R / K_h)^{1/2}$ ;  $r_{root}$  (m) is the radius of root segment (Landsberg and  
8 Fowkes 1978) and  $K_h$  is axial conductivity.  $L_R$  was initially set equal to  $L_P$  and was then  
9 gradually increased to solve the equation for  $L_R$  by iteration.

10 To measure axial conductivity ( $K_h$ ) used to calculate  $L_R$ , the distal end of the root segment  
11 was cut and its terminal 2-mm portion was recut under distilled water. Then  $K_h$  ( $\text{m}^4 \text{s}^{-1} \text{MPa}^{-1}$ )  
12 was calculated as:

$$13 \quad K_h = Q_v / (\Delta P / L)$$

14 where  $\Delta P$  (MPa) is the pressure drop, and  $L$  (m) is the length of the root segment.  $Q_v$  was  
15 measured as for  $L_p$

16

## 17 RESULTS

18 There were two rainless months (June and July) during the dry season of 2003, the main  
19 study period, and the mean air saturation deficit ( $D$ ) increased by about 1KPa between the  
20 beginning and the end of the dry season (Fig. 1a). Consistent with the reduced water input  
21 from precipitation and increased evaporative demand, soil water potentials decreased  
22 substantially during the dry season. In August 2003 soil water potentials were -2.2 MPa and -  
23 1.5 MPa at 20 and 100 cm deep, respectively (Fig. 1b). The insert in Fig. 1b depicts daily

1 time courses of soil water potential ( $\Psi_{\text{soil}}$ ) at 30 and 100 cm deep between 6 and 10 August  
2 2003. There were noticeable daily fluctuations at 30 cm depth without substantial longer term  
3 changes, but  $\Psi_{\text{soil}}$  at 100 cm depth decreased in a nearly continuous manner.

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

12 Patterns of seasonal variations in sap flux differed among species depending on their  
13 leaf phenology (Fig. 3). None of the species studied exhibited reverse sap flux in lateral roots  
14 during the wet season, but as the dry season progressed, *K. coriacea* and *B. crassa*, deciduous  
15 and brevideciduous species respectively, exhibited reverse sap flux in their lateral roots,  
16 particularly at the end of the dry season. Reverse sap flux was not detected in lateral roots of  
17 the evergreen species *S. macrocarpa* and no substantial decrease in stem or root sap flow  
18 occurred during the dry season (Fig. 3 and Table 2). On the other hand, the maximum sap  
19 flux for stems and laterals roots decreased toward the end of the dry season in the deciduous  
20 and brevideciduous species. Consistent with this decline in sap flux in trunks and lateral  
21 roots, the tap root contribution to total daily sap flow in the deciduous and brevideciduous  
22 species increased toward the end of the dry season (Table 2). In contrast, the contribution of

1 the tap root to the total daily trunk sap flow in the evergreen *S. macrocarpa* did not change  
2 significantly from wet to dry season (Table 2).

3 Diagrammatic representations of root distribution for Cerrado trees that hydraulically  
4 lift water, and for species or individuals that do not perform hydraulic lift are represented in  
5 Fig. 4. In some cases one species may have individuals that fit more than one diagrammatic  
6 model of root architecture. Potential differences in root architecture within one species are  
7 expected due to the heterogeneity of nutrient distribution within the soil profile and of soil  
8 physical properties that may modify root growth patterns, Overall, species that showed  
9 hydraulic lift had dimorphic root systems with active roots exploring several soil layers,  
10 while species that did not perform hydraulic lift tended to have mono-morphic roots systems  
11 with roots that tap water from similar soil layers.

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

19 Reverse sap flow in lateral roots of deciduous and brevideciduous species capable of  
20 hydraulic lift increased asymptotically as the difference in water potential between roots and  
21 soil increased (Fig. 6). When the  $\Psi_{\text{soil}}$  to  $\Psi_{\text{root}}$  difference reached a threshold of about 0.8  
22 MPa, the reverse sap flow did not respond to any further increases in the driving force for  
23 water movement (Fig. 6). Reverse sap flow in lateral roots of deciduous and brevideciduous

1 species also increased asymptotically with increasing percentage of nocturnal sap flow  
2 through the main stem (Fig. 7). At the end of the dry season, when nocturnal basal sap flow  
3 represent a relatively large fraction of the total daily sap flow (20 to 30 %), reverse flow in  
4 lateral roots tended to remain constant. The percent loss of total and radial hydraulic  
5 conductivity ( $L_R$ ) in lateral shallow roots between the wet and the dry season decreased  
6 linearly with increasing reverse sap flux in lateral roots across four species studied (Fig. 8 a  
7 and b).

8 Diurnal variations in sap flux were a function of the amount of transpiring leaves in a  
9 deciduous species (*K. coriacea*) (Fig. 9). Reverse sap flux was only observed in one lateral  
10 root at nighttime when *K. coriacea* still had a full crown of leaves during the middle of the  
11 dry season (Fig. 9a). However, after the same tree became leafless one month later, all the  
12 roots studied exhibited reverse sap flux (Fig. 9b). Sap flux was barely detectable in the main  
13 stem at this time. A similar pattern of sap flux was observed in a *K. coriacea* tree with leaves  
14 when transpiration was prevented experimentally (Fig. 9c). Both the roots and stem exhibited  
15 reverse sap flux at night. When the first heavy rains occurred during the wet to dry season  
16 transition, and consequently the soil water potential of the upper soil layers were more  
17 positive than the soil layers below it, water flow from the main stem to deeper roots or from  
18 upper roots to tap roots were not observed (results not shown).

19

## 20 DISCUSSION

### 21 *Relationships between hydraulic lift, spatial patterns of root distribution and leaf phenology*

22 Root systems that explore deep soil layers or large soil volumes are a prerequisite for  
23 sustaining transpiration and carbon fixation during periods of low soil water availability in



1 seasonally dry environments. Cerrado trees in particular, allocate more than 50% of their  
2 biomass belowground (Castro & Kauffman 1998) and explore large soil volumes, with  
3 several species having very deep roots (e.g. Rawistcher 1948; Jackson *et al.* 1999; Oliveira-  
4 Filho *et al.* 1994; Sarmiento, Goldstein & Meinzer 1985; Goldstein, Sarmiento & Meinzer  
5 1985; Meinzer *et al.* 1999; Bucci *et al.* 2005; Franco *et al.* 2005). Nevertheless the broader  
6 functional significance of different patterns of root distribution and their impact on whole  
7 ecosystem processes is still poorly understood.

8         Consistent with differences in their root architecture (monomorphic versus dimorphic  
9 root systems), seasonal changes in the temporal patterns of sap flow differed among species  
10 depending on their leaf phenology. As the dry season progressed, deciduous and  
11 brevideciduous species exhibited reverse sap flow in their lateral roots, particularly at the end  
12 of the dry season, and the contribution of tap roots to transpiration increased substantially. In  
13 this sense, deciduous and brevideciduas species showed facultative behavior, using a  
14 substantial amount of water from deep soil layers during the dry season (up to 57% of total  
15 daily water use) and shallow soil water during the rainy season. The evergreen species did  
16 not have lateral roots with reverse sap flow, and did not show any substantial change in the  
17 partitioning of root flow between the lateral roots and the tap root and on the total amount of  
18 water loss during the dry season, compared to wet season values.

19         Regardless of some differences in vertical partitioning of water uptake during the dry  
20 season, species from all three phenological groups were capable of utilizing relatively deep  
21 soil water. Our findings concerning reliance on deep water sources by both deciduous and  
22 evergreen species during the dry season are consistent with soil water depletion studies in the  
23 Cerrado using time-domain reflectometry (Oliveira *et al.* 2005a) and neutron probes

1 (Quesada *et al.* 2004) showing that soil compartments below 100 cm contribute about 80% of  
2 the total water used during dry season.

### 3 *Determinants of reverse flow in lateral roots*

4 Several studies have found that hydraulic redistribution at the stand level is triggered when  $\Psi$   
5 in the upper soil falls below -0.4 to -0.7 MPa (Caldwell & Richards 1989; Dawson 1993;  
6 Millikin & Bledsoe 2000; Meinzer *et al.* 2004; Brooks *et al.* 2006). However, the relevant  
7 driving force governing the seasonal dynamics of hydraulic lift is the difference between  $\Psi$   
8 soil and  $\Psi_{\text{root}}$  rather than  $\Psi_{\text{soil}}$  alone. Reverse sap flow in lateral roots of three of the  
9 deciduous and brevideciduous species studied increased asymptotically with  $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$ .  
10 When  $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$  increased beyond 0.8 MPa, the reverse sap flow remained nearly  
11 constant despite the increase in the driving force. Multiple factors, including partial loss of  
12 root conductivity during the dry season and decreases in soil hydraulic conductivity were  
13 likely to have contributed to this behavior. The percent loss of total hydraulic conductivity  
14 ( $L_P$ ) and radial conductivity ( $L_R$ ) in shallow lateral roots increased during the dry season.  
15 However, the magnitude of the seasonal decline in  $L_P$  and  $L_R$  was species-specific and  
16 depended on rates of reverse sap flow.

17 Other factors may also partially explain why reverse sap flow in lateral roots became  
18 independent of  $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$  above 0.8 MPa. Nocturnal transpiration is prevalent in  
19 Cerrado woody species during the dry season (Bucci *et al.* 2004; Scholz *et al.* 2007a) and  
20 may represent an additional competing sink for water taken up by deep roots that may  
21 otherwise be released by shallow roots to the upper soil layers. Reverse sap flow in lateral  
22 roots of deciduous and brevideciduous species increased asymptotically with increasing  
23 nocturnal sap flow through the main stem, implying that nocturnal transpiration can limit the

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

### 21 *Downward hydraulic redistribution*

22 In some vegetation types, the first rainfall events after a long dry period can result in  
23 downward hydraulic redistribution from the upper to lower soil layers through roots (Burgess

1 *et al.* 1998; Burgess *et al.* 2001; Smith *et al.* 1999; Oliveira *et al.* 2005b). However, in the  
2 present study none of the five individuals specially fitted with heat pulse sensors during the  
3 dry to rainy season transition period exhibited downward sap flow in the tap root (data not  
4 shown). The following two factors may explain the lack of downward hydraulic  
5 redistribution in the Cerrado species studied: (1) the tap root is exploring deep soil layers  
6 with abundant water and consequently after the first conspicuous rain event during the dry to  
7 wet season transition, the soil water potential gradient between upper soil and deep soil  
8 layers becomes small or nonexistent, (2) Cerrado soils have a very high saturated hydraulic  
9 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  
10 2006) and the infiltration rates are also high (1.26 m h<sup>-1</sup>, Eiyti 2001). Consequently, even in  
11 the absence of a shallow to deep root pathway, the soil water potential gradients developed  
12 during the dry season can be rapidly eliminated after a large rainfall event at the beginning of  
13 the rainy season. Nevertheless, downward hydraulic redistribution may occur in Cerrado  
14 trees under certain conditions. In an earlier study, we recorded a few hours of nocturnal  
15 reverse flow in a tap root of a Cerrado tree after a rainfall event that ended a long rainless  
16 period (Scholz *et al.* 2002). We believe that downward hydraulic redistribution seldom  
17 occurs in Cerrado trees, and when it does, it is a phenomenon of very short duration without  
18 an important role in the hydrological cycle of Neotropical savanna ecosystems.

#### 19 *Functional significance of hydraulic lift*

20 Results from this study showed that the percent loss of total and radial root hydraulic  
21 conductivity in lateral shallow roots between the wet and dry season decreased linearly with  
22 increasing reverse sap flow among four deciduous and brevideciduous species. The relative  
23 permeability of roots to water tends to vary directly with water availability in the soil (Huang

1 & Nobel 1993). This dependence of root  $L_p$  on soil moisture conditions has been referred to  
2 as rectifier-like behavior in roots of desert plants (Nobel & Sanderson 1984), and was  
3 associated with physiological and anatomical changes that led to large decreases in axial and  
4 radial hydraulic conductivity (North & Nobel 1996). In the present study, hydraulic lift and  
5 the associated reverse sap flow in lateral roots were sufficient to maintain root hydraulic  
6 conductivity at a level that prevented complete root rectification. Similarly, Domec *et al.*  
7 (2004) found that partial overnight replenishment of soil water by hydraulic lift in old-growth  
8 ponderosa pine and Douglas-fir stands prevented  $\Psi_{\text{soil}}$  from falling to levels that would have  
9 induced complete loss of water transport capacity in shallow roots compared to stands with  
10 young trees where the magnitude of hydraulic lift was low.

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

1 Species-specific root system architecture could have important implications for  
2 whole-ecosystem water, carbon and nutrient balance. According to the results of our study,  
3 deciduous and brevideciduous species were the only ones with lateral roots exploring nutrient  
4 rich soil layers. These species also have leaf N and P concentrations that are higher than  
5 those of evergreen species (Franco *et al.* 2005), and they represent close to 50 % of the  
6 woody component in Cerrado ecosystems (Lenza & Klink 2006). It is therefore possible that  
7 species with dimorphic root systems can contribute more to nutrient cycling than evergreen  
8 species, not only because they exploit upper soil horizons with higher levels of available  
9 nutrients, but also because hydraulic lift through the release of water into the rhizosphere can  
10 facilitate processes related to mineralization, organic matter decomposition and symbiotic  
11 relationships

12

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For Peer Review

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

4

Species	Leaf phenology	Height (m)	Basal diameter (cm)	Number of trees
<i>S. macrocarpa</i>	Evergreen	3.9 $\pm$ 0.2	11.2 $\pm$ 0.9	6
<i>S. paniculatum</i>	Evergreen	6.0 $\pm$ 0.3	15.3 $\pm$ 1.1	4
<i>V. elliptica</i>	Evergreen	4.0 $\pm$ 0.2	5.1 $\pm$ 0.1	5
<i>B. crassa</i>	Brevideciduous	2.1 $\pm$ 0.1	9.0 $\pm$ 0.4	35
<i>B. salicifolius</i>	Brevideciduous	4.0 $\pm$ 0.1	9.6 $\pm$ 0.6	35
<i>D. miscolobium</i>	Brevideciduous	4.2 $\pm$ 0.3	12.6 $\pm$ 1.3	5
<i>A. tomentosum</i>	Deciduous	3.2 $\pm$ 0.3	4.4 $\pm$ 0.3	5
<i>K. coriacea</i>	Deciduous	2.6 $\pm$ 0.2	5.6 $\pm$ 0.5	35
<i>Q. parviflora</i>	Deciduous	2.6 $\pm$ 0.2	5.2 $\pm$ 0.3	25

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1 Table 2. Seasonal variation in sap flow ( $\text{cm}^3 \text{ day}^{-1}$ ) in the trunk, one lateral root and the  
 2 tap root of one individual of *K. coriacea*, *B. crassa* and *S. macrocarpa*. Negative values  
 3 of sap flow indicate reverse flow (from root to soil). Values in parentheses represent the  
 4 percentage of lateral root or tap root total daily sap flow compared to the trunk total daily  
 5 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%)	3.8 (2.5%)
	Tap root	156 (13%)	-3.5 (0.6%) 273 (47%)	-3.9 (2.6%) 70 (47%)
<i>B. crassa</i> Brevideciduous	Trunk	553	336	128
	Lateral root	27 (4.9%)	8.8 (2.6%)	-15.6 (12%)
	Tap root	166 (30%)	-13.5 (4%) 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%)

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## 1 FIGURE LEGENDS

2 Figure 1. Seasonal variation in mean monthly (a) precipitation and air saturation deficit  
3 ( $D$ ) from January 2002 to December 2003, and (b) soil water potential at 10, 20, 30 and  
4 100 cm depth, for several days of the 2003 dry season at the IBGE research station. The  
5 insert in panel (b) shows diurnal fluctuations of soil water potential for 5 days at the end  
6 of the dry season (August) at 30 and 100 cm depth. Bars in panel (a) represent  
7 precipitation and the solid line represents  $D$ . Bars in panel (b) are mean monthly values  
8 ( $\pm$ SE) of four replicate sensors per depth during 3 or 4 days per month.

9

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

15

16 Figure 3. Representative seasonal variation in sap flux in the main stem, tap root and  
17 lateral roots of *K. coriacea*, a deciduous species (a,b,c), *B. crassa*, a brevideciduous  
18 species (d,e,f) and *S. macrocarpa*, an evergreen species (g,h,i) from the wet season (  
19 November 2002), early dry season (June 2003) and at the peak of the dry season (August  
20 2003).

21

22 Figure 4. Diagrammatic representations of root architecture in Cerrado trees for species  
23 or individuals that hydraulically lift water (A to E) and for species or individuals that did

1 not show evidence of hydraulic lift (F to I). The frequency of individuals with that  
2 particular type of root system architecture/total number of studied individuals (Fq root)  
3 and the frequency of individuals exhibiting hydraulic lift/total number of individuals  
4 studied (Fq HL) are indicated. Major active roots, either tap roots or lateral roots with  
5 secondary growth that are easily observed during an excavation, are represented

6

7 Figure 5. (a) Log of difference between the hydrogen isotope ratio ( $\delta D$ ) of water obtained  
8 from lateral roots of the treated plants (tap root supplied with deuterated water) and  $\delta D$  of  
9 root water ( $\delta D_{\min}$ ) from the control plants whose tap roots were not supplied with  
10 deuterated water, and (b) Log of difference between  $\delta D$  of soil water around the roots of  
11 the treated plants and  $\delta D$  of soil water around roots of control plants ( $\delta D_{\min}$ ). Actual  $\delta D$   
12 values equivalent to those indicated on the log scale are shown on the right axis. Soil and  
13 root water with  $\delta D$  values within the gray area are not significantly different from values  
14 of control plants; those outside the gray area are significantly different from values of  
15 control plants at  $P < 0.1$ . The species studied were: *Qp*: *Qualea parviflora* ( $\diamond$ ), *Bs*:  
16 *Blepharocalyx salicifolius* ( $\square$ ), *Bc*: *Byrsonima crassa* ( $\bullet$ ), *Kc*: *Kielmeyera coriacea*  
17 ( $\blacktriangle$ ) and *At*: *Aspidosperma tomentosum* ( $\nabla$ ).

18

19 Figure 6. Normalized total daily reverse sap flow in lateral roots of three woody species  
20 in relation to the absolute value of the difference between soil and root water potential  
21 ( $|\Psi_{\text{soil}} - \Psi_{\text{root}}|$ ) for different days between the beginning and end of the dry season of  
22 2003. Reverse sap flow was normalized respect to the maximum value reached for a  
23 particular root during the dry season. Values of  $\Psi_{\text{soil}}$  were measured psychrometrically

1 for soil layers at the same depth where the root was found. The line is an exponential  
2 function fitted to the data ( $y = -0.41 + 1.41*(1 - \exp(-3.38x))$ ,  $P < 0.0001$ ). All species for  
3 which root water potential data were available for different times during the dry season  
4 are shown.

5

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

13

14 Figure 8. (a) Percent loss of total root hydraulic conductance ( $L_p$ ) and (b) percent loss of  
15 radial conductance ( $L_R$ ) between wet and dry season in relation to total daily reverse sap  
16 flux in lateral roots at the peak of the dry season. Values of reverse sap flux are means  
17 ( $\pm$ SE) of three to six roots in different trees. Values of  $L_p$  and  $L_R$  are means of three to six  
18 different roots measured during the wet seasons (January 2004) and the dry (August  
19 2004) and the in different trees. For *K. coriacea* only two roots were obtained during the  
20 dry season. A linear regression was fitted to each relationship (a)  $y = 77 = 0.13x$ ,  
21  $P = 0.035$ ; (b)  $y = 74.5 - 0.17x$ ,  $P = 0.05$ . Symbols are: (●) *B. crassa*, (▲) *K. coriacea*, (□)  
22 *B. salicifolius* and (◇) *Q. parviflora*

23

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

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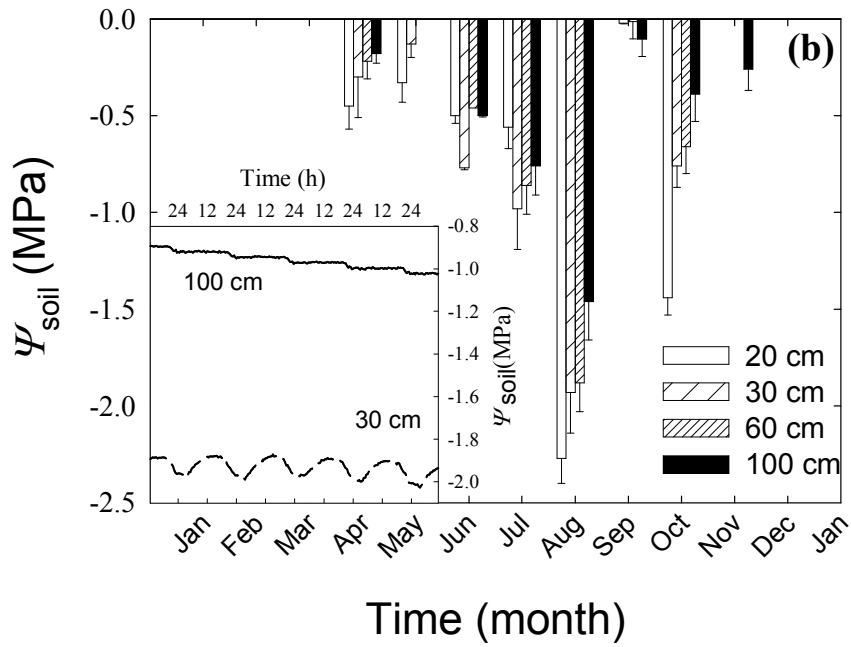
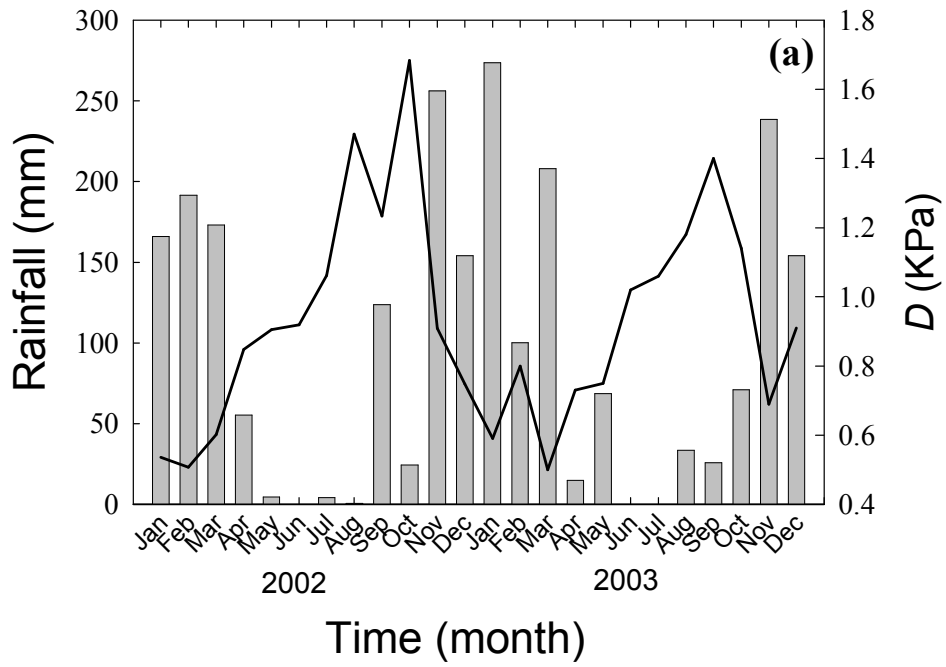
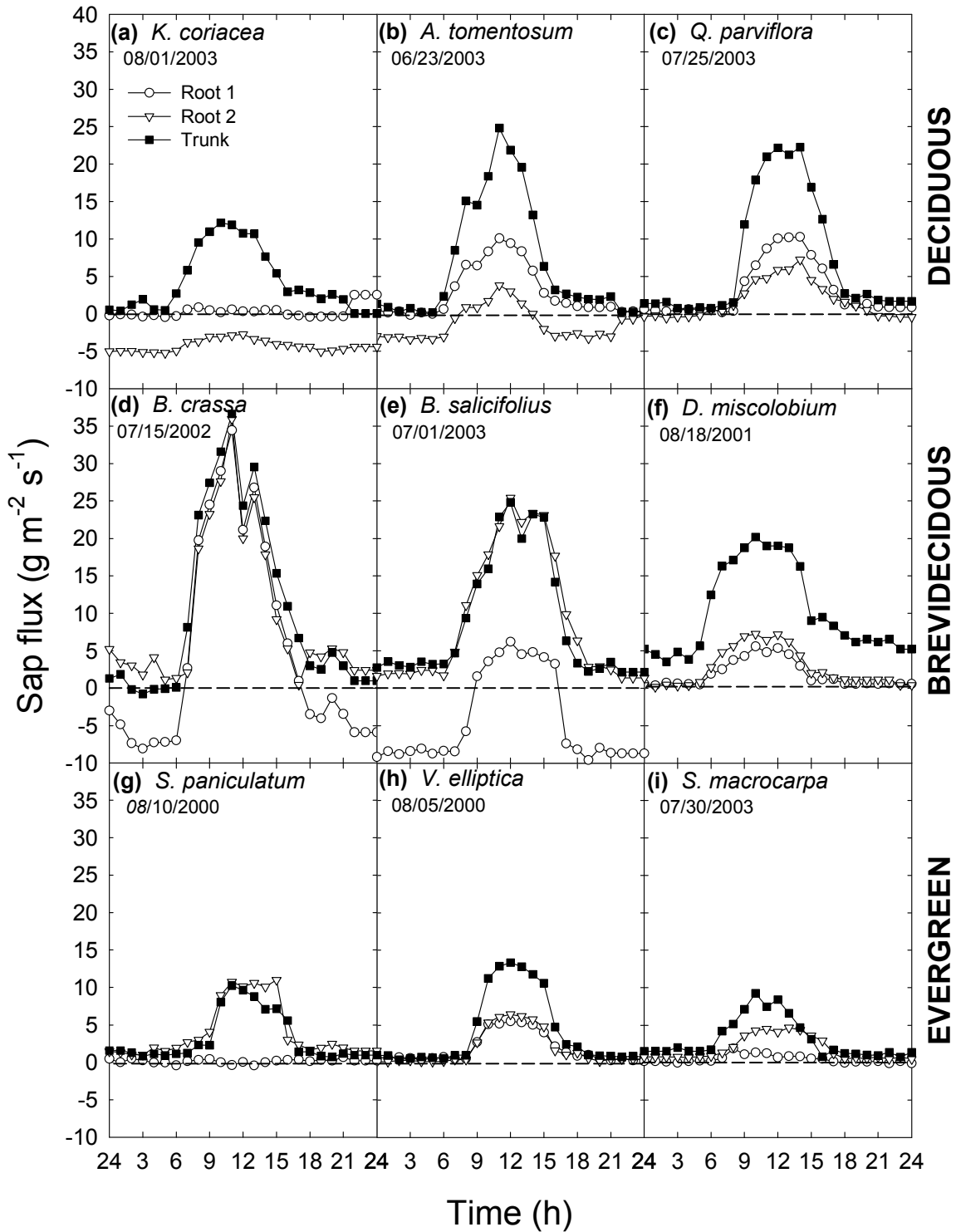


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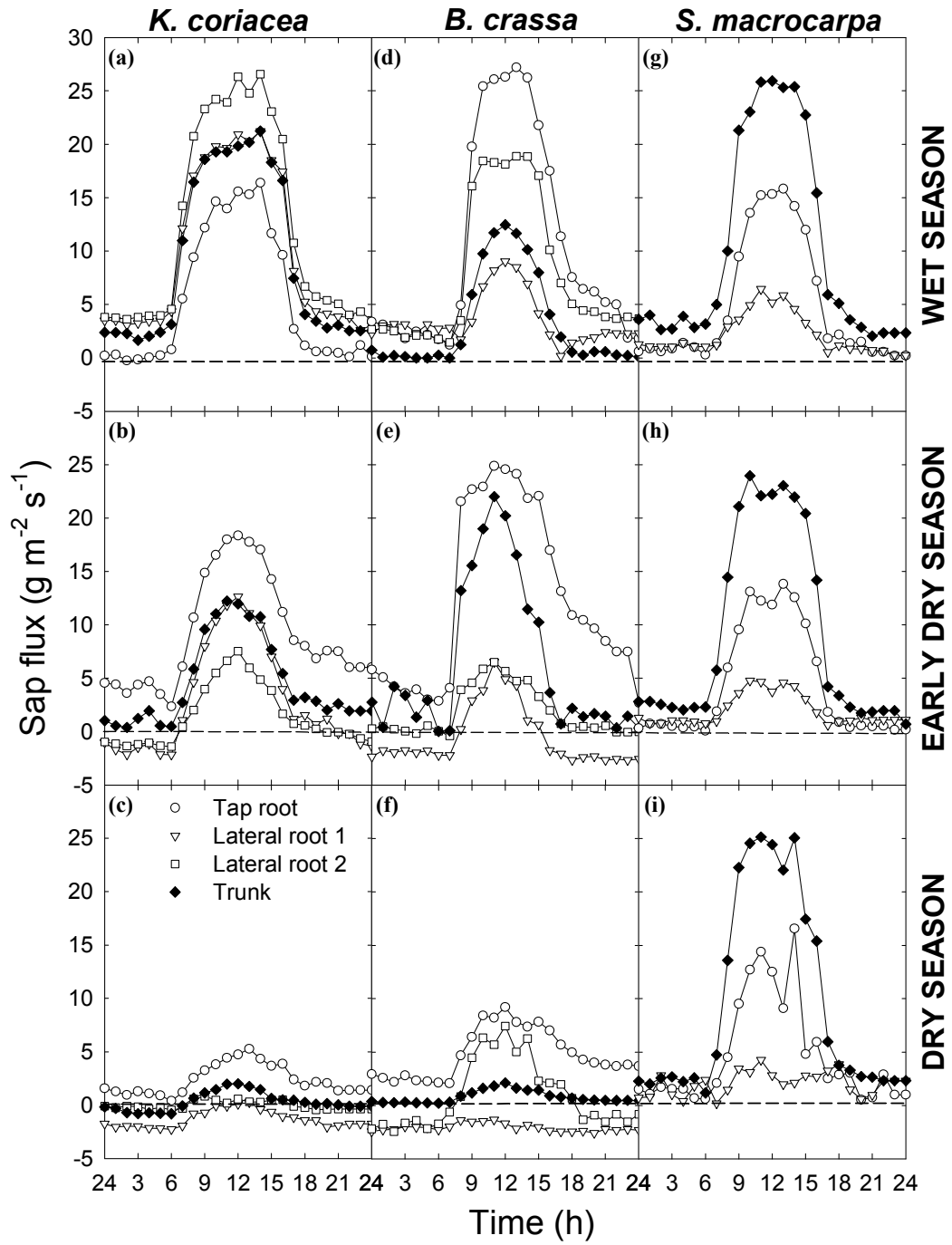
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Figure 2.

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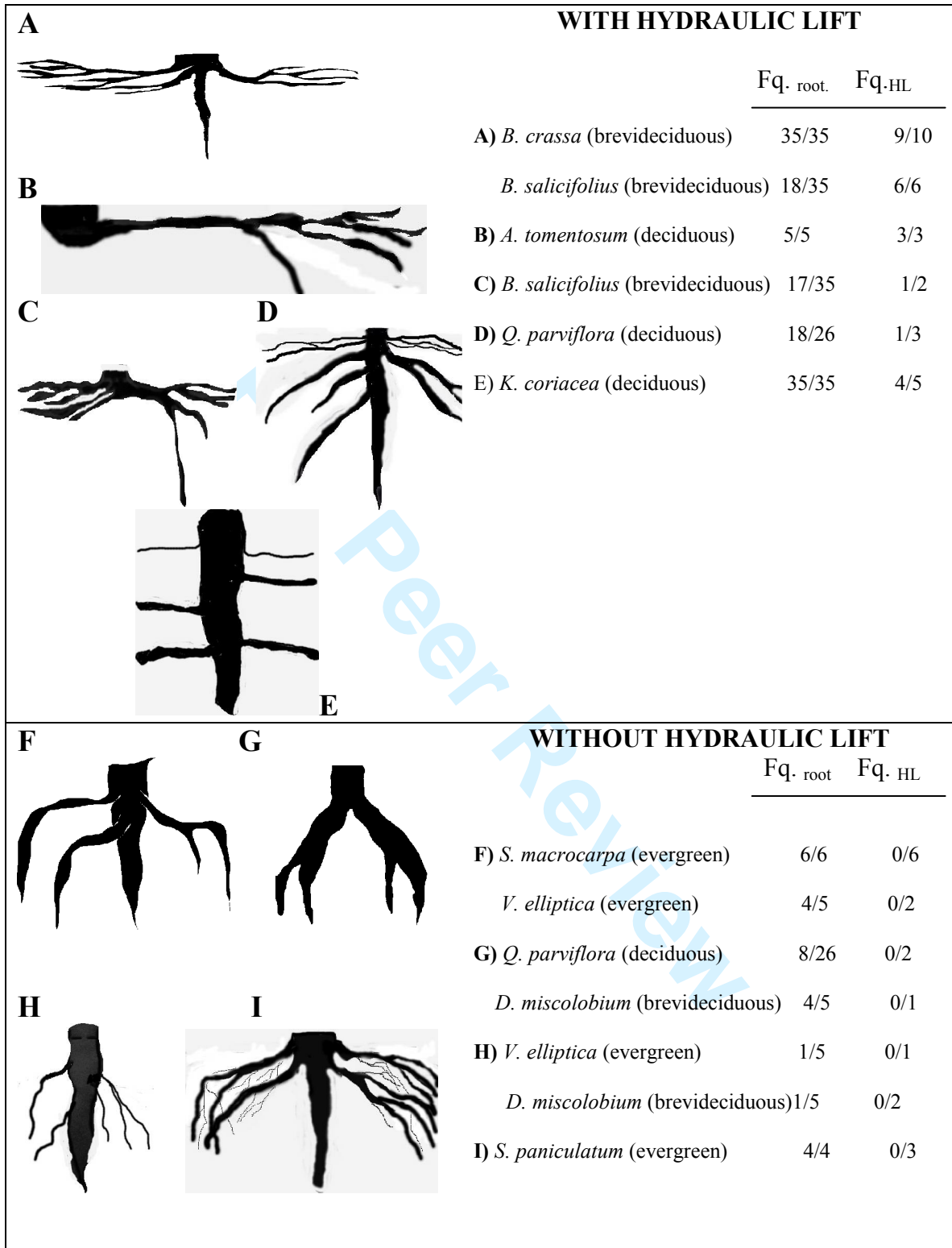
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Figure 3



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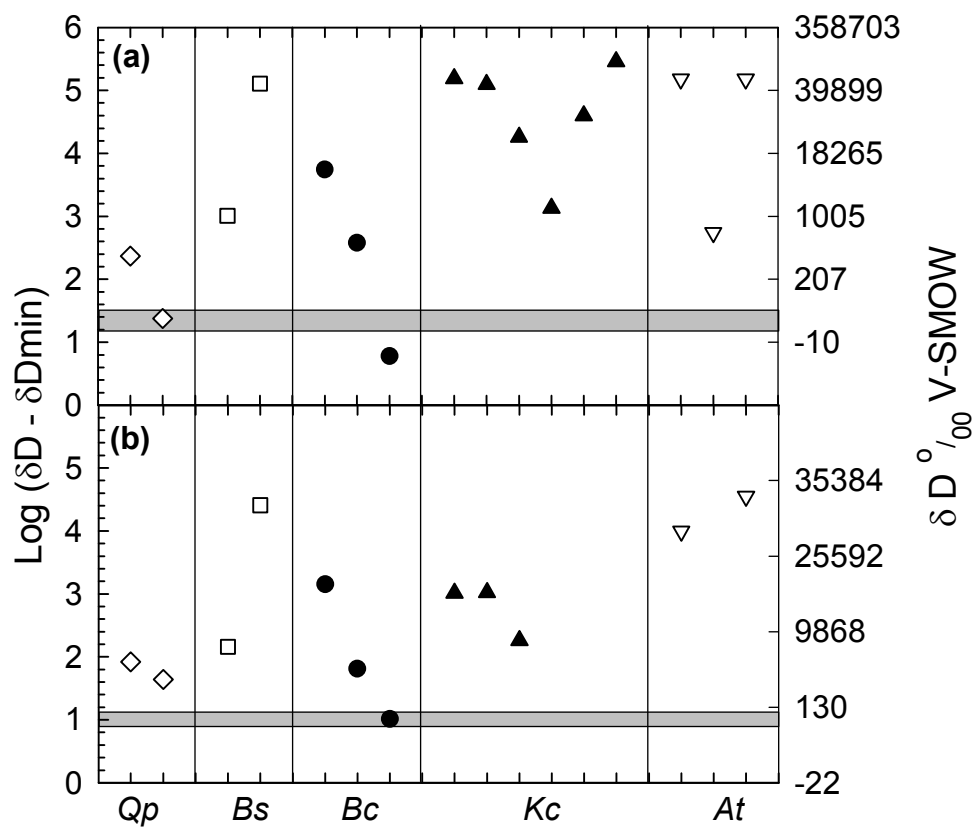
Figure 4



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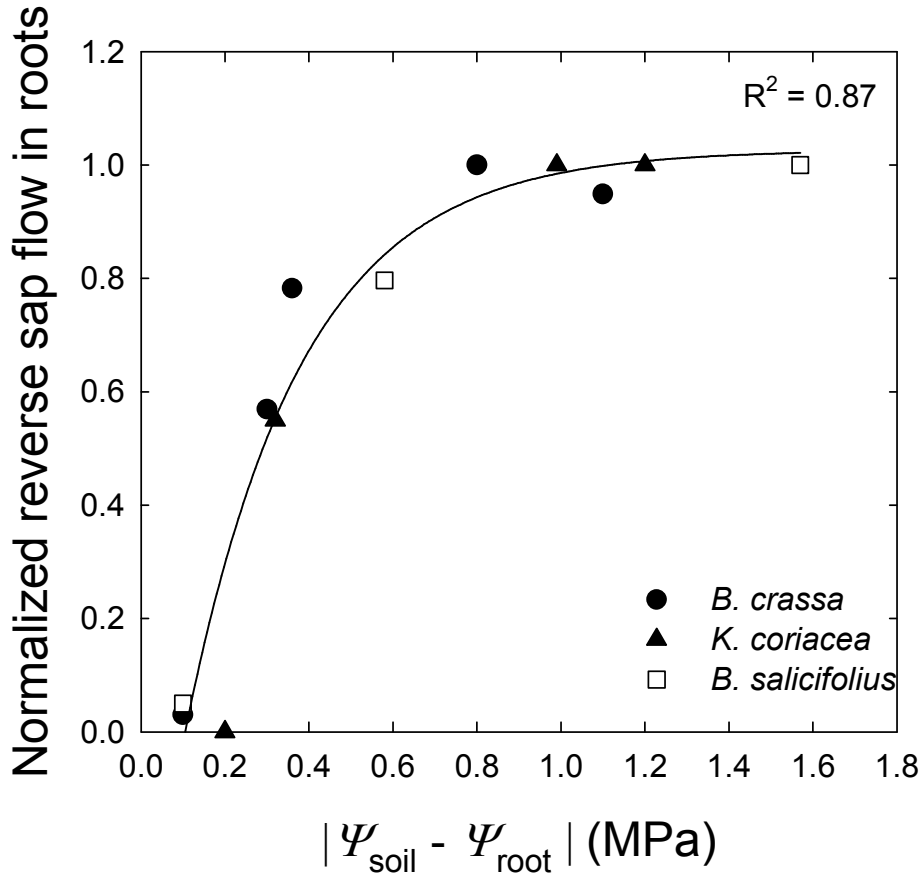
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Figure 5.

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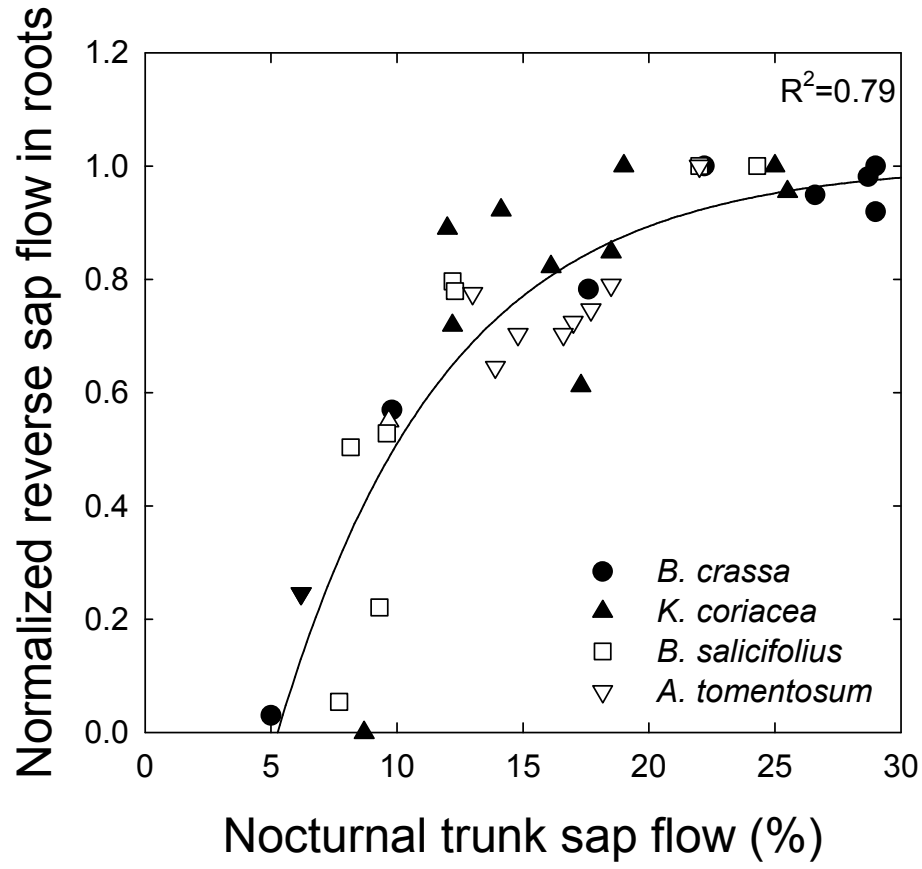


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Figure 6.

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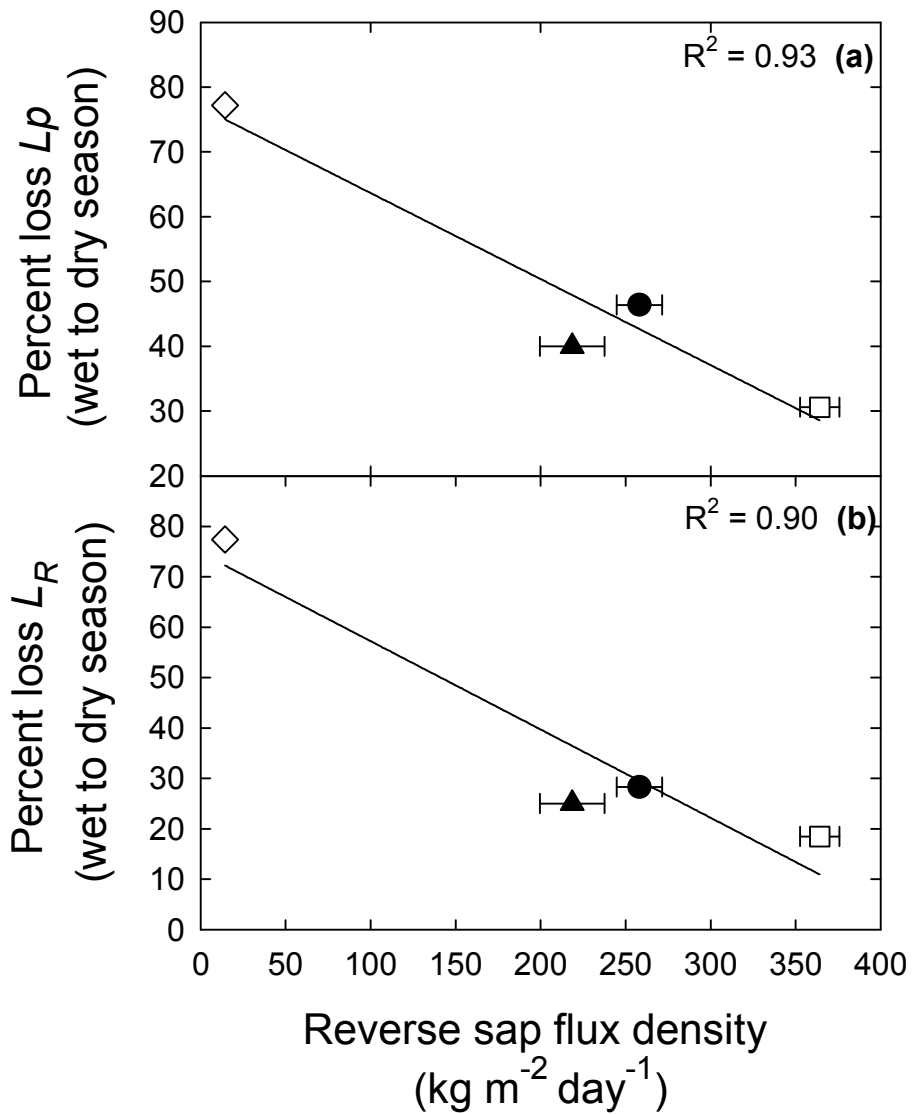
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Figure 7.

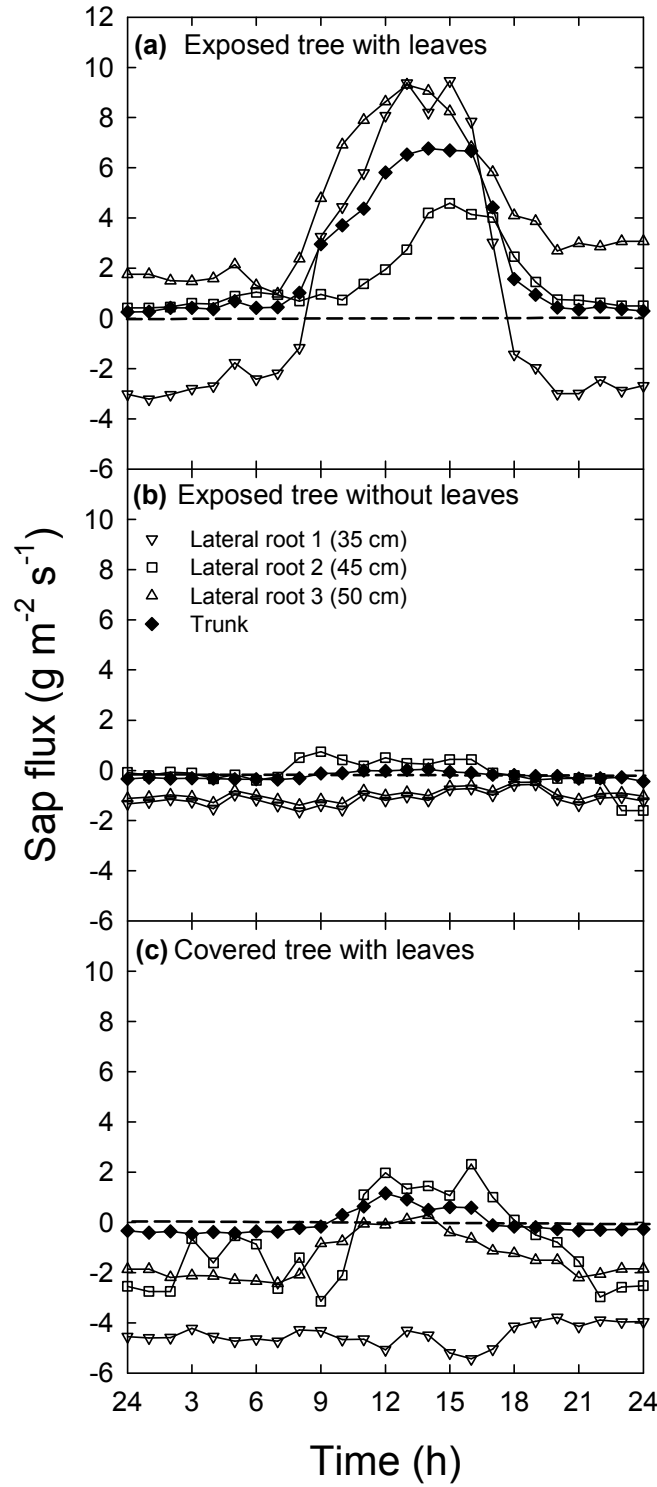
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Figure 8.



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Figure 9.