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Hydraulic redistribution of soil water by neotropical savanna trees

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Summary The magnitude and direction of water transport by the roots of eight dominant Brazilian savanna (Cerrado) woody species were determined with a heat pulse system that allowed bidirectional measurements of sap flow. The patterns of sap flow observed during the dry season in species with dimorphic root systems were consistent with the occurrence of hydraulic redistribution of soil water, the movement of water from moist to drier regions of the soil profile via plant roots. In these species, shallow roots exhibited positive sap flow (from the soil into the plant) during the day and negative sap flow (from the plant into the soil) during the night. Sap flow in the taproots was positive throughout the 24-h period. Diel fluctuations in soil water potential, with maximum values occurring at night, provided evidence for partial rewetting of upper soil layers by water released from shallow roots. In other species, shallow roots exhibited negative sap flow during both the day and night, indicating that hydraulic redistribution was occurring continuously. A third sap flow pattern was observed at the end of the dry season after a heavy rainfall event when sap flow became negative in the taproot, and positive in the small roots, indicating movement of water from upper soil layers into shallow roots, and then into taproots and deeper soil layers. Experimental manipulations employed to evaluate the response of hydraulic redistribution to changes in plant and environmental conditions included watering the soil surface above shallow roots, decreasing transpiration by covering the plant and cutting roots where probes were inserted. Natural and manipulated patterns of sap flow in roots and stems were consistent with passive movement of water toward competing sinks in the soil and plant. Because dry shallow soil layers were often a stronger sink than the shoot, we suggest that the presence of a dimorphic root system in deciduous species may play a role in facilitating leaf expansion near the end of the dry season when the soil surrounding shallow lateral roots is still dry.

Keywords: Cerrado vegetation, heat pulse method, hydraulic lift, roots, sap flow.

Introduction

The movement of water from moist to drier portions of the soil profile via plant root systems has been termed hydraulic lift (Richards and Caldwell 1987, Caldwell et al. 1989). The direction of water movement is typically upward, from deeper to shallower soil layers. However, recent studies of sap flow in taproots and lateral roots of trees have demonstrated that roots can also redistribute water from the surface to deeper soil layers (Burgess et al. 1998, 2001*a*, Smith et al. 1999). The process is thought to be largely passive, requiring only a gradient in soil water potential (Ψ_{soil}), a more positive Ψ in the root xylem than in surrounding dry soil layers, and a relatively low resistance to reverse flow through and efflux from the roots. Because it can be bidirectional (upward and downward) and is apparently passive, "hydraulic redistribution" has been proposed as a more comprehensive term for the phenomenon (Burgess et al. 1998). Hydraulic redistribution usually occurs at night when transpiration has diminished sufficiently to allow the Ψ in the roots to exceed that in the drier portions of the soil profile. It is believed that hydraulic redistribution can contribute significantly both to the water balance of the plant responsible for it, and to that of neighboring plants of other species (Dawson 1993). Water released from roots into drier soil layers may be reabsorbed when transpiration exceeds water uptake by deep roots alone (Richards and Caldwell 1987). In addition to its positive influence on plant water balance during dry periods, hydraulic redistribution may also enhance nutrient uptake by fine roots located in the relatively nutrient-rich upper portion of the soil profile, which normally undergoes severe desiccation in environments characterized by a long dry season (Caldwell et al. 1998), and may contribute to maintenance of the activity of mycorrhizae and symbiotic nitrogen-fixing bacteria as the bulk soil in the upper portion of the profile dries.

The belowground structure of tropical savanna ecosystems is typically described as two-layered, with water and nutrients being limiting resources (Walker and Noy-Meir 1982, Knoop and Walker 1985, Sarmiento et al. 1985). According to this model, originally proposed by Walker and Noy-Meir (1982), shallow-rooted grasses are superior competitors for water in the upper part of the soil profile, whereas woody plants have exclusive access to a deeper and more reliable water source. Consistent with this model of tropical savannas, evergreen woody plants in Venezuelan savannas maintain a constant predawn and minimum leaf water potential during the long dry season, whereas herbaceous plants die back as their water potential declines in parallel with that of the upper soil layers (Goldstein et al. 1985, Sarmiento et al. 1985).

Although the tropical savannas of northern South America are characterized by relatively low woody plant diversity, the savannas of central Brazil (Cerrado) are remarkably complex and rich in endemic woody species. More than 500 species of trees and large shrubs are present 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). Based on hydrogen isotope analyses of soil and plant water, Jackson et al. (1999) concluded that Cerrado trees extract water over a wide range of soil depths. In addition, hydrogen isotope ratios in the soil profile were consistent with hydraulic lifting of water. The coexistence of such a large number of species with different rooting patterns and the possible redistribution of soil water by roots suggests that soil water partitioning and dynamics in the Cerrado are more complex than the patterns predicted by the two-layered model.

The Cerrado region is subjected to a prolonged rainless season leading to severe drying in the upper portion of the soil profile (Franco 1998). It is characterized by the presence of deeply rooted woody species, some with dimorphic root systems, and presumably shallow-rooted herbaceous species. This combination of features should present favorable circumstances under which to evaluate the occurrence and magnitude of hydraulic redistribution. The objective of this study was to determine the pattern and direction of water uptake/transfer by the roots of eight dominant Cerrado woody species during the dry season and the dry-to-wet season transition. The species were selected to represent a range of root system architectures and vegetative phenologies. A heat pulse system that allowed the direction of root and stem sap flow to be measured was used (Marshall 1958, Burgess et al. 1998). Experimental manipulations employed to evaluate the response of hydraulic redistribution to changes in plant or environmental conditions included watering the soil surface above shallow roots and decreasing transpiration by covering the plant. Diel courses of water potential in the upper soil layers were also measured.

Materials and methods

Site description and environmental measurements

Cerrado vegetation comprises three principal physiognomic types: *cerradao*, a medium to tall woodland with a closed or semi-closed canopy; *cerrado sensu-stricto*, a savanna with abundant evergreen and brevi-deciduous trees and an herbaceous understory; and *campo sujo*, an open savanna with scattered trees and shrubs. Cerrado vegetation contains different combinations of these three vegetation types organized spatially along gradients of decreasing abundance of woody plants from *cerradao* to *cerrado sensu-stricto* to *campo sujo* over distances of only a few kilometers.

The present study was conducted in a *cerrado sensu-stricto* stand at the Instituto Brasileiro de Geografia e Estatística (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasilia (15°56′ S, 47°53′ W, altitude 1100 m). Mean 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 with diurnal temperature ranges of 20 °C being common during the dry season. The soils are deep oxisols consisting of about 72% clay. Despite their high percentage of clay, the soils behave as coarser-textured soils and are extremely well drained.

Eight species from 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. Frodin (Araliaceae) is an evergreen tree up to 10 m tall with palmately compound leaves on branches clustered near the apex of the stem; *Byrsonima crassa* Nied. (Malpighiaceae) is a brevi-deciduous shrub or tree up to 5 m tall with large scleromorphic simple leaves; *Styrax ferrugineus* Nees & Mart. (Styracaceae) is an evergreen tree up to 15 m tall with medium size simple leaves; *Dalbergia miscolobium* Benth. (Leguminosae) is a deciduous 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; *Blepharocalix salicifolius* (H.B. & K.) Berg. (Myrtaceae) is a brevi-deciduous tree up to 10 m tall with small simple leaves; and *Vochysia elliptica* Mart. (Vochysiaceae) is an evergreen tree species up to 5 m tall with simple leaves and short petioles.

Roots of representative individuals of the eight dominant tree species were excavated to determine their rooting pattern. Conspicuously dimorphic root systems consisting of many relatively small lateral roots located between ~2 and 10 cm below the soil surface, and one larger taproot that penetrated the soil vertically from the stem base, were observed in *B. crassa*, *S. ferrugineus* and *B. salicifolius*. *Dalbergia miscolobium* had a single or a few primary or descending roots without conspicuous superficial lateral roots. Root systems of *S. paniculatum* and *Q. parviflora* resembled the fibrous root systems of grasses in having a large number of different size roots with no identifiable primary or taproot. Intermediate root system types were observed in *V. elliptica* and *S. macrocarpa*.

Soil water potential (Ψ_{soil}) was determined with screen-cage thermocouple psychrometers (Model PST-55, Wescor, Logan, UT) at 12 and 23 cm depth, about 1 m away from the bole of several woody plants. Measurements were obtained manually at 3-h intervals with a dew point hygrometer (Model HR33-T, Wescor) operating in the dew point mode. Diurnal fluctuations in soil temperature at the measurement depths were small and temperature gradients in the psychrometers were small enough to permit corrections to be applied. Soil volumetric water content was measured with 1.2-m multi-segment profiling time domain reflectometry (TDR) probes (Type A, Environmental Sensors, Victoria, Canada). The probes were interrogated and read with an MP-917 TDR unit (Environmental Sensors). Leaf water potential (Ψ_{leaf}) of *B. salicifolius* was measured with a pressure chamber (PMS, Corvallis, OR) on the same day that soil water potentials were monitored. Measurements were made several times during the day on three leaves from three individuals.

Relative humidity and air temperature were monitored continuously with a probe (HMP35C, Campbell Scientific, Logan, UT) placed at 2 m height near the center of the study site. Data were obtained every 10 s and 10-min means were recorded with a data logger (CR10X, Campbell Scientific). Air saturation deficit (ASD) was calculated as the difference between saturation vapor pressure at the air temperature and ambient vapor pressure.

Sap flow measurements

A heat pulse system based on the early work of Marshall (1958) and recently further developed by Burgess et al. (1998) was used to measure sap flow in roots and stems. A 6-s pulse of heat was produced by applying a known voltage across a 38 Ω line heater fitted inside a 10 µl glass micropipette and inserted in a hypodermic needle. The resulting increase in temperature was measured by two copper-constantan temperature probes placed at equal distances (0.6 cm) up- and downstream from the heater (Burgess et al. 1998). The thermocouples were connected by duplex insulated copper-constantan extension cable to a data logger (CR10X, Campbell Scientific) sealed inside an insulated box to minimize temperature differences between the thermocouple inputs. The data logger controlled the duration of the heat pulse. The temperature probes and heater were coated with a thermal dissipation paste and inserted in holes drilled radially into a root or stem using a template to minimize spacing errors.

The heat pulse velocity (V_h) was calculated according to Marshall (1958) as:

$$V_h = D/x \ln(v_1/v_2), \tag{1}$$

where D is thermal diffusivity of wet wood, x is distance between the heat source (line heater) and the temperature sensors, and v_1 and v_2 are the increase in temperature after the heat pulse, at equidistant points downstream and upstream, respectively, from the heater. Calculations were based on measurements made between 60 and 100 s after the release of the heat pulse, when the ratio of v_1 and v_2 was most stable (Burgess et al. 2001*b*). Thermal diffusivity of wet wood was calculated for each species according to a procedure suggested by Burgess et al. (2001*b*) using an equation presented by Marshall (1958):

$$D = K_{\text{sw}}/\rho_{\text{sw}}c_{\text{sw}}, \tag{2}$$

where K_{sw} is thermal conductivity, ρ_{sw} is density and c_{sw} is specific heat capacity of sapwood. Thermal conductivity was estimated using a modification by Burgess et al. (2001*b*) of an equation presented by Swanson (1983):

$$K_{\text{sw}} = K_s m \frac{\rho_{\text{dw}}}{\rho_s} + K_{\text{dw}}\left(1 - m\frac{\rho_{\text{dw}}}{\rho_s}\right), \tag{3}$$

where K_s and K_{dw} are thermal conductivity of sap (water) and dry wood, respectively, m is water fraction of sapwood, ρ_{dw} is density of dry wood and ρ_s is density of sap. The thermal conductivity of dry wood (W m^{-1} °C^{-1}) was calculated according to Swanson (1983) as:

$$K_{\text{dw}} = 4.184 \times 10^{-2}\,(21 - 20F_v), \tag{4}$$

where F_v is void fraction of sapwood defined as one minus the sum of the solid and liquid fractions. The specific heat capacity of sapwood, c_{sw}, was calculated from the specific heat capacities of its water and solid constituents (Anonymous 1995). Root samples from each species were collected prior to dawn for determination of the above parameters. The values of D obtained with this method ranged from 0.0016 to 0.0018 cm^2 s^{-1}. Heat pulses were applied every 30 min, after xylem temperatures around the temperature probes returned to ambient. Sap flow from the soil into the plant was considered to be positive and flow away from the stem base toward the soil was considered to be negative.

Heat pulse velocity was corrected for xylem wounding associated with probe installation based on the estimated wound widths and coefficients provided by Burgess et al. (2001*b*). Sap velocity (V_s) was then calculated from the corrected heat pulse velocity (V_c) using a modification (Barrett et al. 1995) of Marshall's (1958) equation:

$$V_s = V_c\rho_{\text{dw}}(c_{\text{dw}} + mc_s)/(\rho_s c_s), \tag{5}$$

where c_{dw} and c_s are specific heat capacities of dry wood and sap, respectively. Empirical calibration of V_s was carried out with excised branches by comparing V_s calculated as described above, and gravimetric measurements of V_s. A nearly perfect one to one relationship ($y = 0.996x - 0.034$, $r^2 = 0.998$) was obtained between calculated and measured V_s over a flow range of –5 to +50 cm^3 h^{-1}.

Volumetric sap flux (V_{sf}) in the stem was obtained by multiplying V_s by the sapwood cross-sectional area. The active xylem area for water transport was obtained by injecting indigo carmine dye near the location where sap flow was measured and determining the sapwood area from the pattern of staining (Meinzer et al. 1999, 2001). The active xylem area of the roots was taken as the cross-sectional area of the root minus the pith area (where present) and bark thickness.

Sap flow was measured simultaneously in three locations on each plant selected for study: the main stem; a taproot or other large descending root; and a smaller shallow root. Roots around the base of the main stem were excavated with minimal disturbance until two adequate roots were found. Wooden walkways were used to access excavation sites in order to avoid damaging surrounding grasses and other herbaceous vegetation. Superficial lateral roots were partially excavated using small digging tools to create openings in the soil approximately 10 to 50 cm in diameter and 25 cm deep. Taproots and other descending roots were accessed by first excavating to ~50 cm depth near the base of the stem, then excavating horizontally. The diameters of the roots and stems were measured with calipers. After installing the probes in the two types of roots and in the stem near its base, they were thermally insulated, and the roots were immediately re-covered with soil. Some plants were experimentally manipulated in one of the following ways: (1) the plant was covered with opaque plastic bags to minimize transpirational water loss; or (2) portions of a small root that exhibited reverse flow during both the day and night were irrigated to simulate a rainfall event of 50 mm. In some cases, repeatability of the flow patterns observed in a given plant was verified by reinstalling the probes in a comparable pair of roots on the same plant. 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 root. Corrected values of reverse flow did not differ substantially from uncorrected values. Severing of taproots and major descending roots not exhibiting negative flow was avoided to minimize damage to the study plants. The preceding measurements were carried out during the peak of the 2000 dry season (end of July and August), and during the transition between the dry and wet seasons (end of August until September 6, 2000). The first recorded rainfall event occurred on August 29, 2000.

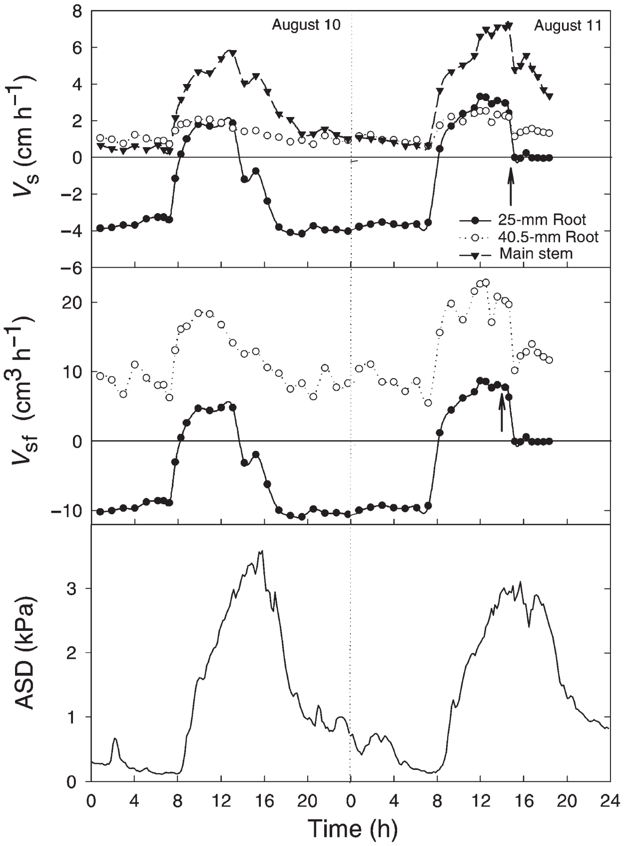

Figure 1. Sap velocity (V_s) and volumetric sap flux (V_{sf}) in 25- and 40.5-mm-diameter roots and in the main stem of a *Byrsonima crassa* tree during August 10 and most of August 11, 2000, at the IBGE research station. The individual was in full leaf, but the leaves had begun to senesce. The 25-mm root was sectioned at 1430 h (arrows). Air saturation deficit (ASD) during the measurement period is shown.

Results

Reverse sap flow was detected in roots of four of the eight Cerrado species studied. Representative observations are presented for *B. crassa*, *B. salicifolius* and *S. ferrugineus*.

During the peak of the dry season, both positive and negative flows were observed in a small (25 mm) *B. crassa* root, which ran parallel to the soil surface (Figure 1). Sap flow in this root was always negative at night and rapidly became positive soon after sunrise, but began to reverse direction again shortly after midday, reaching its most negative values by sunset. Its mean nighttime sap velocity and volumetric sap flux were about –4 cm h^{-1} and –10 cm^3 h^{-1}, respectively. A larger taproot (40.5 mm) on the same plant, and the main stem, exhibited low positive flows at night and relatively large positive flows during the day when ASD was high (Figure 1). The negative sap flow at night in the superficial root and the positive flow in the taproot were consistent with hydraulic lifting of water from the lower to the upper soil layers. On August 11, the 25-mm root was cut at the proximal and distal ends of the section where the probes were installed, resulting in a sudden decrease in sap velocity to 0 cm h^{-1} after correction for the zero flow offset value (0.60 cm h^{-1}).

A similar diel pattern of sap flow was observed in *S. ferrugineus* (Figure 2). The sap flow of the smaller lateral root was negative during the night, but the larger taproot and the stem always had positive flows. To determine if the flow patterns were representative of those in roots of similar size on the same plant, the probes of the heat pulse system were transferred at 1030 h on August 15 to other roots of similar size. The probes in the 22-mm root were installed in a 17-mm root and the probes in the 34-mm root were installed in a 31-mm root. The pattern and magnitude of sap flux density and volumetric sap flux remained similar after the transfer of the probes.

From August 1 to 3, the sap flow in the stem and a larger (57 mm) root of a *B. salicifolius* tree was slightly positive or zero during the night and positive during the day (Figure 3). In a smaller 45-mm root, however, sap flow was negative during the night and positive only during periods of high evaporative demand (i.e., at midday). On the morning of August 4, the tree was entirely covered with opaque plastic bags to minimize transpiration, and one large branch was removed. This manipulation eliminated the large diurnal fluctuations in sap veloc-

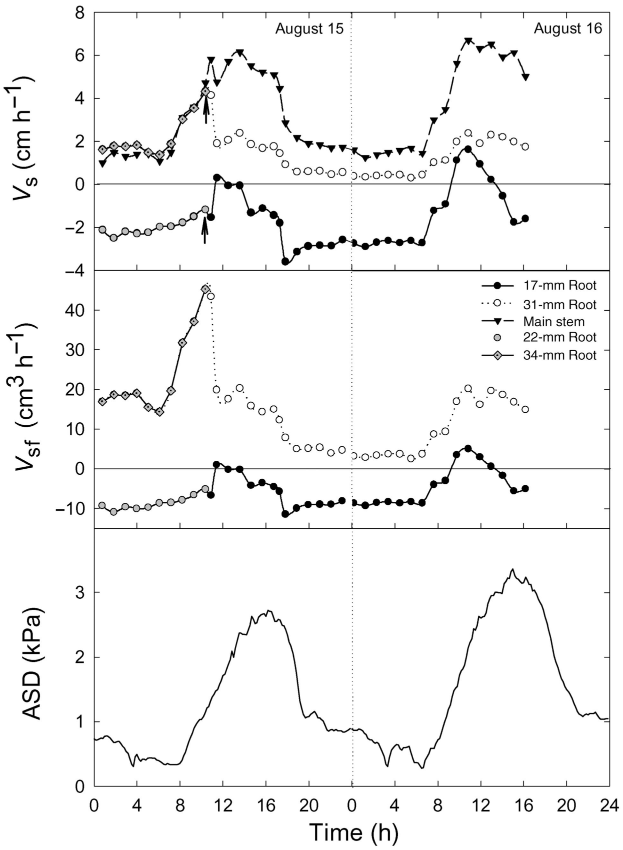

Figure 2. Sap velocity (V_s) and volumetric sap flux (V_{sf}) in small and larger roots and in the main stem of a *Styrax ferrugineus* tree during August 15 and most of August 16, 2000, at the IBGE research station. On August 15 at 1030 h (arrows) the probes of the heat pulse system were transferred to a second pair of roots of similar size. Air saturation deficit (ASD) during the measurement period is shown.

ity, except briefly on August 5, when one of the bags covering a branch was accidentally opened, resulting in a small increase in flow until the bag was closed again. During this period, sap velocity in the 45-mm root always remained negative at about –4 cm h^{-1}. During the afternoon of August 6, the plastic bags were removed, allowing the plant to transpire freely again, and the diel fluctuations reappeared. However, the maximum positive sap velocities in roots and stem did not return to their previous values because of the reduction in leaf surface area following branch removal.

An experiment was performed to evaluate the speed of sap flow reversal from negative to positive after soil water potential around small superficial roots was increased by irrigation. Two small roots of a *B. salicifolius* tree initially exhibited negative sap flow throughout the day, suggesting that soil water potential near the surface was more negative than leaf water potential, even during periods of high transpiration (Figure 4). On the evening of August 9, water was applied to the soil surface above the 19-mm root (Figure 4, arrow). On the following day, the sap flux density of the irrigated root rapidly became positive after sunrise and reached its maximum in the early afternoon before dropping sharply to around zero in the late afternoon and early evening. Patterns of sap flow in the non-irrigated root and trunk did not change.

Sap flow in two roots and the stem of *B. crassa* was monitored for 13 days during the dry-to-wet season transition period (Figure 5). Before the first rainfall event (Days 1 to 4), sap flow was negative in a small 12.5-mm root and positive in a 36.5-mm root and in the main stem. A heavy rain event (44.6 mm) that lasted for about 24 h occurred during Day 5 of the measurement period (notice that during this day ASD remained near 0 kPa). During the rainfall, the sap flow pattern of the stem and small root was reversed, with the 12.5-mm root

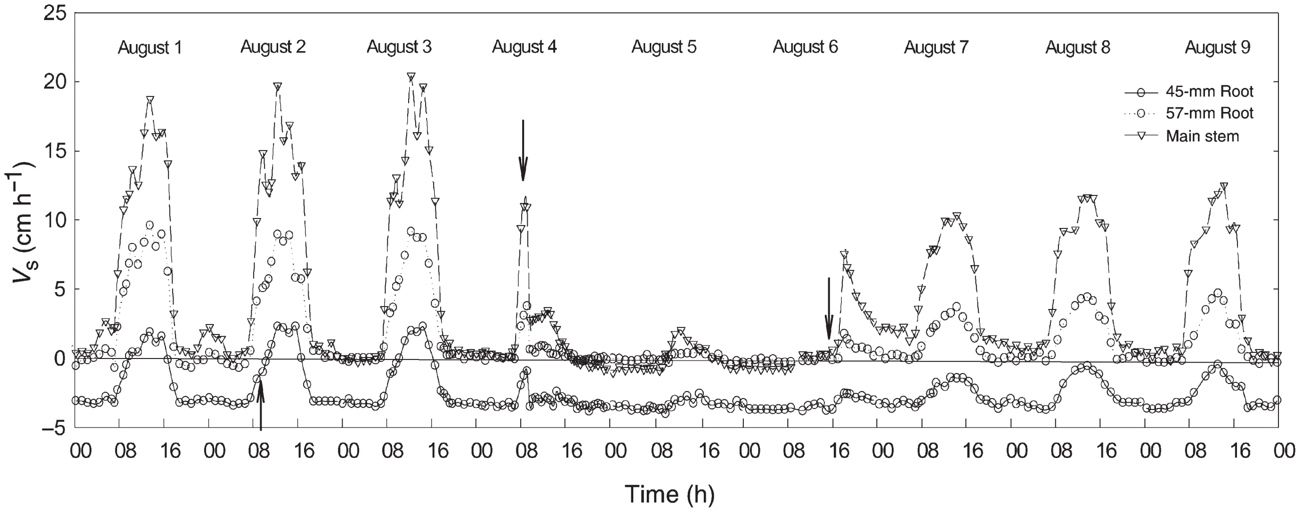

Figure 3. Sap velocity (V_s) in small and larger roots and in the main stem of a *Blepharocalyx salicifolius* tree from August 1 to 9, 2000, at the IBGE research station. A new crop of fully expanded leaves was present. On August 2 (arrow), the probes of the heat pulse system were transferred to another section of the same 45-mm root. On August 4 (arrow), the plant was covered with bags to restrict transpiration. The bags were removed on August 6 (arrow).

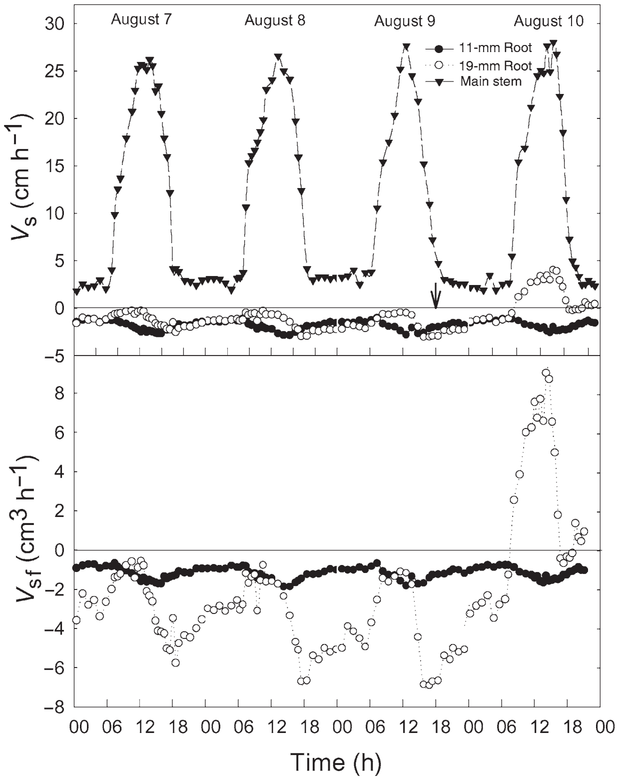

Figure 4. Sap velocity (V_s) in 11- and 19-mm-diameter roots and in the main stem of a *Blepharocalyx salicifolius* tree, and volumetric sap flux (V_{sf}) in the roots from August 7 to 10, 2000, at the IBGE research station. A new crop of fully expanded leaves was present. On August 9, a 6 m^2 area of soil above the 19-mm root was watered (arrow).

having a positive sap flow and the stem having a negative sap flow. The stem sap velocity dropped to about –1.5 cm h^{-1} at about midday and then increased slowly until the next morning. Another major rain event occurred on Day 10 of the measurement period. After this rain event, sap flow in the 36.5-mm root became negative at night, suggesting that water was moving downward through the large taproot into deeper soil layers. The preceding responses are depicted in more detail in Figure 6. Before rainfall (August 27), sap flow in the 12.5-mm root was negative during both the day and night, whereas sap flow in the large root and stem was near zero at night and closely tracked the diel course of ASD. On September 4, following two major rainfall events, sap flow in the 12.5-mm root was positive during both the day and night, whereas flow in the 36.5-mm root was negative at night.

Before rainfall, soil water content was lowest in the upper soil layers. For example, the volumetric water content was 10% in the 15–30-cm soil layer and 14.5% in the 90–120-cm layer. After the rain event of August 29, the water content of the 0–15-cm soil layer increased rapidly to 25% in 6 days, whereas the water content of the deeper soil layers increased slowly. Rewetting of the surface soil by rainfall therefore reversed the soil water gradient. Consistent with the differences in soil volumetric water content before rain, the soil water potential near two trees was more negative at 11.5 cm than at 23 cm depth (Figure 7). The soil water potential exhibited marked diel fluctuations with minimum values occurring around midday and maximum values occurring during the night. For one of the species (*B. salicifolius*), leaf water potential and sap flow in a small lateral root were measured simultaneously with soil water potentials. Root sap velocity appeared to be linearly related to the difference between soil and leaf water potential (Figure 8). Reverse flow became more pronounced as Ψ_{soil} became increasingly more negative than Ψ_{leaf}. Positive flow was observed only when Ψ_{leaf} was more negative or slightly less negative than Ψ_{soil}.

Discussion

Measurements of sap flow in roots and stems were consistent with hydraulic redistribution of soil water in four of the eight Cerrado species studied (data not shown for *Q. parviflora*). In these species, three main patterns of diurnal sap flow were observed during the dry season and during the dry-to-wet season transition. In the first pattern, small, shallow roots exhibited positive sap flow during the day and negative sap flow during the night, whereas sap flow in the taproots was positive throughout the 24-h period. In this case, partial rewetting of the upper soil layers by hydraulic redistribution is expected to occur only at night when plant water potential is less negative than the water potential of the upper soil layers. Diel changes in soil water potential measured near plants exhibiting this pattern of root sap flow were also consistent with the existence of hydraulic redistribution. The volumetric sap flux away from the stem base toward the soil ranged from 2 to 11 cm^3 h^{-1}, depending on the root size and species. The second pattern of root sap flow was similar to the first, except that the soil water potential was apparently low enough to induce continuous negative sap flow in the small roots. In this case, hydraulic redistribution and partial rewetting of the upper soil layers is expected to occur continuously (Burgess et al. 2000). Continuous reverse flow has also been observed in taproots following the beginning of the wet season (Smith et al. 1999).

The third pattern of root sap flow was observed at the end of the dry season after rewetting of the surface soil by a heavy rainfall event. Sap flow became negative in the taproot, and positive in the small roots at night. Clearly, soil water moved into shallow roots, and therefore from upper soil layers into deeper roots and deeper soil layers. A similar downward pattern of water transfer by hydraulic redistribution has been observed in roots of other species following rainfall at the beginning of the wet season (Burgess et al. 1998, 2001*a*, Smith et al. 1999). Rapid downward transfer of water via roots following rainfall during the dry-to-wet season transition may facilitate establishment of woody plants by promoting early growth of deep roots in dry soil layers and modifying availability of nutrient resources at depth (Burgess et al. 2001*a*). We also observed a transient reverse (downward) flow in the main stem of *B. crassa* during a major 24-h rainfall event (Figure 5). This behavior was consistent with transient reversal of the normal

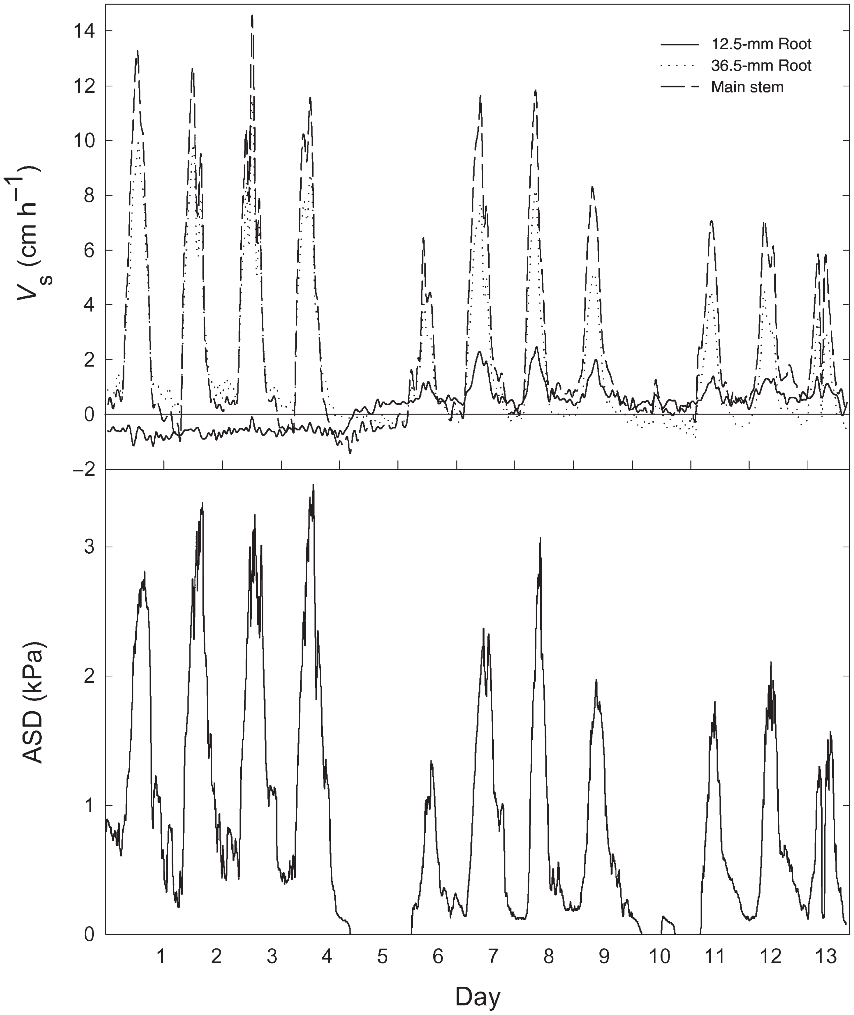

Figure 5. Sap velocity (V_s) in 12.5- and 36.5-mm-diameter roots and in the main stem of a *Byrsonima crassa* tree measured from August 25 to September 6, 2000 at the IBGE research station. The individual had a full complement of senescing leaves and began to expand new leaves during the measurement period. Air saturation deficit (ASD) during the measurement period is shown. Heavy rainfall events occurred during August 29 (Day 5) and September 3 (Day 10).

soil-to-leaf water potential gradient, probably associated with the presence of water on the foliage. All three patterns of root sap flow observed were consistent with passive movement of water driven by changing water potential gradients along the soil-to-leaf continuum.

As indicated above, not all of the woody Cerrado species studied had clearly dimorphic root systems or patterns of root sap flow, consistent with the occurrence of hydraulic redistribution of soil water. In *D. miscolobium*, *S. macrocarpa* and *V. elliptica*, for example, sap flow was always positive in both smaller and larger roots throughout the entire 24-h period (data not shown). It is possible that under drier conditions than those that prevailed in the present study, further decreases in the soil water potential would induce negative sap flow in the superficial roots of these species. In *B. salicifolius*, the sap flow from small roots was negative during both the day and the night, implying that the water potential of the surrounding soil was lower than that of the small roots even during periods of high transpiration. The minimum leaf water potential of this species was about −1.7 MPa during the study period, and the minimum water potential of the 0–23-cm soil layer was about −2.0 MPa (Figure 7). The minimum water potential of the small superficial roots was probably substantially less negative than that of the shoot. Thus, the shoot and dry surface soil layers appeared to act as competing sinks for water lifted hydraulically by deep roots, with the relative strength of these sinks determining the direction of water flow in superficial roots (Figure 8). The occurrence of a slightly positive flow in a surface root of *B. salicifolius*, even when Ψ_{soil} was slightly more negative than Ψ_{leaf} (Figure 8), may have been attributable to less negative values of Ψ_{soil} in the vicinity of the root than in the soil surrounding the soil psychrometers, or to an offset between psychrometric measurements of Ψ_{soil} and measurements of Ψ_{leaf} obtained with the pressure chamber. Nevertheless, the highly significant linear relationship between sap flow in superficial roots and the soil-to-leaf water potential difference points to the passive nature of the hydraulic redistribution process whose relative magnitude can be estimated from the relative strengths of the shoot and soil sinks.

The magnitude of the diel changes in soil water potential in this study was similar to that observed in other studies, where hydraulic redistribution was observed (Richards and Caldwell

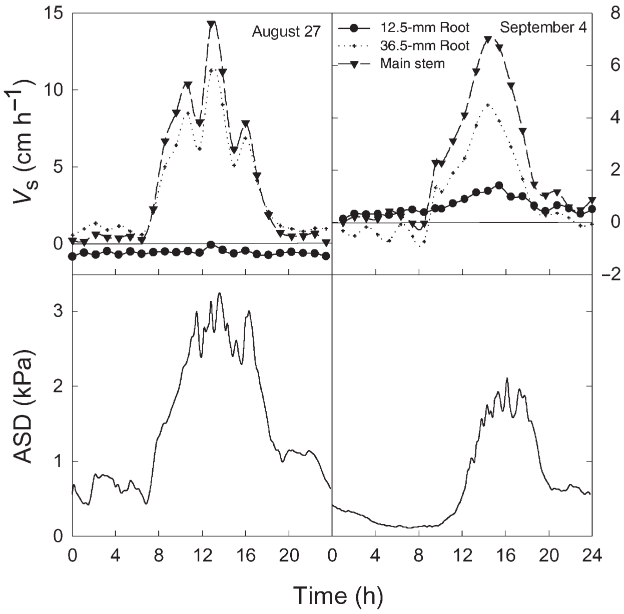

Figure 6. Diel courses of air saturation deficit (ASD) and sap velocity (V_s) in 12.5- and 36.5-mm-diameter roots and in the main stem of a *Byrsonima crassa* tree on August 27 and September 4, 2000 at the IBGE research station.

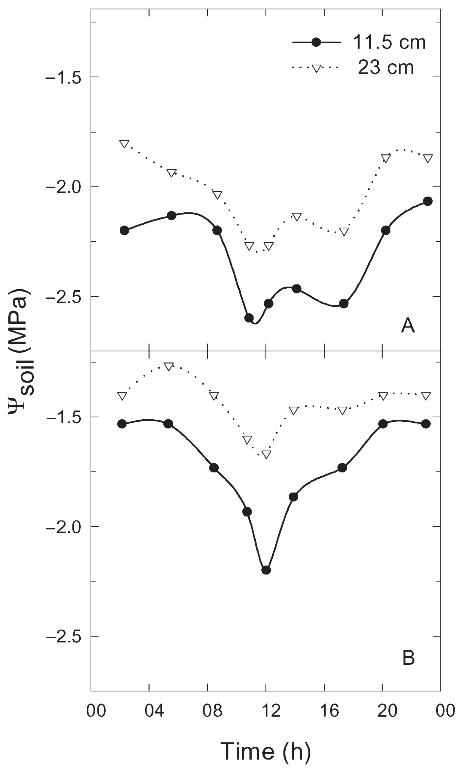

Figure 7. Soil water potential (Ψ_{soil}) at 11.5 and 23.0 cm depth near the bole of a *Byrsonima crassa* (A) and a *Blepharocalyx salicifolius* (B) plant on August 20, 2000 at the IBGE research station.

1987, Dawson 1993, Millikin Ishikawa and Bledsoe 2000). Apparently, soil water potentials were not low enough to cause root rectification (unidirectional flow) or cavitation to occur, preventing sap flow from superficial lateral roots into the soil. Root rectification is a common phenomenon in desert plants, and is associated with both physiological and anatomical changes that lead to large decreases in axial and radial hydraulic conductivity (North and Nobel 1996). Nobel and Sanderson (1984) reported a very large and rapid decrease in radial hydraulic conductivity in two desert succulents when their roots were subjected to drastic drying (Ψ_{soil} = –93.6 MPa). However, with smaller changes in Ψ_{soil}, radial hydraulic conductivity apparently does not decrease enough to completely curtail water loss (Richards and Caldwell 1987). If root rectification or cavitation were to occur, then even if the water potential gradient between root and soil were favorable for water movement out of the small diameter roots into drier, upper soil layers, negative sap flow would be negligible. Hydraulic redistribution may help to maintain the soil water potential near the root surface at values high enough to prevent rectification and cavitation.

Woody Cerrado plants are known for their deep root systems (e.g., Sarmiento 1984). Some Cerrado species, such as *Andira humilis* Benth., have roots that can reach a depth of 18 m (Rawitscher 1948). Species in which root biomass is comparable to the aboveground biomass are also common (Abdala et al. 1998). In a review of the scant literature about the distribution of underground biomass in neotropical savannas, Sarmiento (1984) concluded that the root systems of neotropical savanna trees can be characterized as generally consisting of a dense network of horizontal roots growing at depths of 20 to 50 cm, and larger roots that penetrate deeply into the soil. A much more complex pattern of root distribution, ranging from relatively shallow-rooted to deep-rooted, is found in the savannas of central Brazil owing to the high spe-

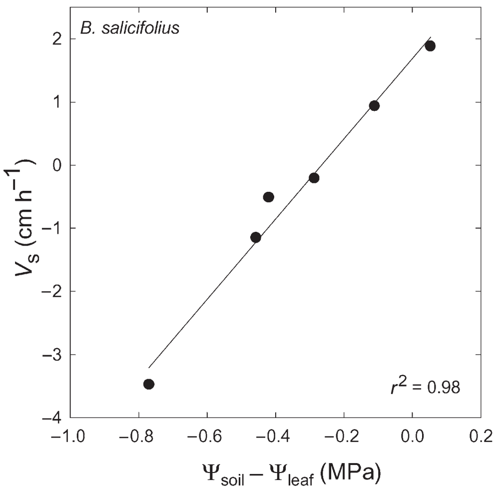

Figure 8. Sap velocity (V_s) measured in a small root of *Blepharocalyx salicifolius* in relation to the soil-to-leaf water potential difference ($\Psi_{soil} - \Psi_{leaf}$). The line is a linear regression fitted to the data. Values of Ψ_{soil} were obtained from the mean measurements at 11.5 and 23 cm depth.

cies diversity of the woody component (Rawitscher 1948, Jackson et al. 1999). The multiple patterns of root sap flow observed in the present study are consistent with a wide range of root system architecture among woody Cerrado species. Deeply rooted Cerrado trees and shrubs are not limited by lack of soil water during the dry season, as indicated by relatively small seasonal variations in leaf water status and similar relationships between maximum sap flow and stem sapwood area for both wet and dry seasons (Meinzer et al. 1999). Despite access to relatively abundant soil water throughout the entire year, transpiration of both evergreen and deciduous Cerrado trees is tightly regulated on a diurnal basis during both dry and wet seasons. Transpiration typically increases sharply in the morning, briefly attains a maximum value before midday (usually between 0930 and 1100 h), and then decreases sharply despite steadily increasing irradiance and vapor pressure deficit. This pattern does not appear to be directly related to plant water status but to independent stomatal adjustment to diurnal variations in whole-plant hydraulic conductance (Meinzer et al. 1999).

Deciduous Brazilian Cerrado tree species appear to have access to deeper, and, therefore, more reliable water sources than evergreen species (Jackson et al. 1999). This observation may appear counterintuitive at first sight, but is consistent with the leaf phenology of these species, characterized by production of new cohorts of leaves before the onset of the rainy season. Although some deciduous Cerrado species remain leafless for only a few days, others remain leafless for several weeks during the dry season. In the latter species, the presence of deep roots in addition to superficial lateral roots may play a critical role in facilitating leaf expansion near the end of the dry season when the soil surrounding shallow lateral roots is still dry. Dimorphic root systems may thus be more commonly associated with the deciduous rather than evergreen habit in woody Cerrado species.

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