

## Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species

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**Summary** The impact of nocturnal water loss and recharge of stem water storage on predawn disequilibrium between leaf ( $\Psi_L$ ) and soil ( $\Psi_S$ ) water potentials was studied in three dominant tropical savanna woody species in central Brazil (Cerrado). Sap flow continued throughout the night during the dry season and contributed from 13 to 28% of total daily transpiration. During the dry season,  $\Psi_L$  was substantially less negative in covered transpiring leaves, throughout the day and night, than in exposed leaves. Before dawn, differences in  $\Psi_L$  between covered and exposed leaves were about 0.4 MPa. When relationships between sap flow and  $\Psi_L$  of exposed leaves were extrapolated to zero flow, the resulting values of  $\Psi_L$  (a proxy of weighted mean soil water potential) in two of the species were similar to predawn values of covered leaves. Consistent with substantial nocturnal sap flow, stomatal conductance ( $g_s$ ) never dropped below  $40 \text{ mmol m}^{-2} \text{ s}^{-1}$  at night, and in some cases, rose to as much as  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$  before the end of the dark period. Nocturnal  $g_s$  decreased linearly with increasing air saturation deficit ( $D$ ), but there were species-specific differences in the slopes of the relationships between nocturnal  $g_s$  and  $D$ . Withdrawal and recharge of water from stem storage compartments were assessed by monitoring diel fluctuations of stem diameter with electronic dendrometers. Stem water storage compartments tended to recharge faster when nocturnal transpiration was reduced by covering the entire plant. Water potential of covered leaves did not stabilize in any of the plants before the end of the dark period, suggesting that, even in covered plants, water storage tissues were not fully rehydrated by dawn. Patterns of sap flow and expansion and contraction of stems reflected the dynamics of water movement during utilization and recharge of stem water storage tissues. This study showed that nighttime transpiration and recharge of internal

water storage contribute to predawn disequilibrium in water potential between leaves and soil in neotropical savanna woody plants.

**Keywords:** capacitance, nocturnal transpiration, sap flow, soil–plant–atmosphere continuum, stomata.

### Introduction

Stomata are thought to minimize transpiration relative to photosynthetic carbon gain and keep transpiration rates consistent with the efficiency of water supply to the leaves (Cowan and Farquhar 1977, Sperry 2000). From this perspective, non-CAM plants should have very low stomatal conductance ( $g_s$ ) at night to prevent transpirational water loss because they do not rely on dark  $\text{CO}_2$  fixation. Negligible or low nocturnal transpiration is assumed to allow leaf ( $\Psi_L$ ) and soil ( $\Psi_S$ ) water potentials to equilibrate before dawn, permitting use of predawn  $\Psi_L$  as a surrogate for  $\Psi_S$  (Ritchie and Hinckley 1975, Hinckley et al. 1978, Richter 1997). However, if processes such as nighttime transpiration prevent equilibration along the soil-to-leaf continuum, predawn  $\Psi_L$  may be significantly more negative than  $\Psi_S$  (Donovan et al. 1999, 2001). A correct estimate of  $\Psi_S$  is key in calculating the driving forces of water movement along the soil–plant–atmosphere continuum. Information on nighttime transpiration may help assess if equilibration along this continuum can be achieved before dawn. Despite its importance, little information exists on the relationship between nocturnal water loss and predawn water potential disequilibrium between soil and leaves in tropical trees.

Nocturnal transpiration has been studied in relatively few species because it is assumed that stomata are uniformly closed

ed at night or that water vapor near the leaf surface is at or near saturation. However, some recent studies with temperate woody species indicate that, under certain environmental conditions, nocturnal water loss can be relatively high (Benyon 1999, Donovan et al. 1999, Oren et al. 1999, Sellin 1999). In one extreme case, the contribution of nocturnal water loss to total daily water loss was about 50% (Feild and Holbrook 2000). In Brazilian savanna sites, nighttime values of relative humidity as low as 40 to 50% during the dry season can result in substantial nocturnal transpiration rates if stomata are not completely closed.

Stems function both as pathways for long distance water transport and as water storage compartments. When  $\Psi_L$  drops as transpiration increases in the early morning, water may move from storage into the transpiration stream, helping to minimize temporal imbalances between water supply and demand and temporarily slowing the decline in  $\Psi_L$  (Holbrook 1995). Taller trees tend to have greater storage capacities which may help compensate for increases in axial resistance with tree height (Goldstein et al. 1998). Water stored in stem tissues can contribute from 6 to 50% of the total water loss by transpiration during a 24-h cycle (e.g., Waring and Running 1978, Tyree and Yang 1990, Goldstein et al. 1998, Phillips et al. 2003). Refilling of water storage compartments usually occurs during the late afternoon and at night when evaporative water loss is low, but it can also occur during the daytime if the vapor pressure difference between leaves and air is small (Goldstein et al. 1998). Nocturnal transpiration may prevent the complete recharge of internal water storage compartments, decreasing the water available internally and consequently limiting the supply of water to transpiring leaves at the beginning of the next day (Donovan et al. 2003). A complete rehydration of the stem water storage compartments is a prerequisite for achieving water potential equilibrium between leaf and soil before the end of the dark period.

In the present study, the occurrence and magnitude of nocturnal transpiration and the dynamics of nighttime recharge of internal water storage compartments were evaluated in three dominant woody species of Neotropical savannas in central Brazil (Cerrado) to determine their impact on overnight equilibration of plant water potential and  $\Psi_s$ . Sap flow, stomatal conductance ( $g_s$ ),  $\Psi_L$ , environmental variables and diurnal changes in stem diameter were measured at the peak of the dry season. Leaf water potentials were also measured during the wet season. Field manipulations were performed to restrict nocturnal transpiration in some plants. Because it could be an additional factor contributing to predawn water potential disequilibrium in savanna plants, the magnitude of reverse flow of sap in stems and the conditions associated with it were investigated with a heat pulse system that measured both the volumetric flow and its direction.

## Materials and Methods

### Study site and plant material

The study was conducted in a savanna site with intermediate tree density (*campo cerrado*) at the Instituto Brasileiro de

Geografia e Estatística (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasília (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. 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 common during the dry season. The soils are deep oxisols consisting of about 72% clay. Despite their high clay content, the soils behave as coarser-textured soils and are extremely well drained.

Three evergreen species among the 25 woody species with the highest measured importance value indices (Felfili et al. 1998) were selected for the study: *Styrax ferrugineus* Ness et Mair. (Styracaceae), *Roupala montana* Aubl. (Proteaceae), and *Oouratea hexasperma* (St. Hil.) Baill. (Ochnaceae). New leaves are produced during the last part of the dry season. Measurements were made at the end of the dry season on new fully expanded leaves. The height of the individuals studied ranged from 2.50 to 2.70 m in *S. ferrugineus*, from 1.90 to 2.15 m in *R. montana* and from 1.65 to 1.70 m in *O. hexasperma*. The diameter at 30 cm above soil surface ranged from 4.5 to 4.7 cm in *S. ferrugineus*, from 4.6 to 5.0 cm in *R. montana* and from 4.5 to 4.9 cm in *O. hexasperma*. Information on the patterns of water uptake of these species can be found in Jackson et al. (1999).

### Environmental variables

Relative humidity and air temperature were monitored continuously with a probe (HMP35C, Campbell Scientific, Logan, UT) placed at a height of 4 m near the center of the study site. Data were obtained every 10-s, and 10-min means were recorded with a datalogger (CR10X, Campbell Scientific). Air saturation deficit ( $D$ ) was calculated as the difference between saturation vapor pressure at the air temperature and ambient vapor pressure. Soil water potentials were monitored with soil psychrometers (PST-55, Wescor, Logan, UT) at soil depths of 20, 30, 60 and 100 cm. Measurements were made every 30 min with a 30-s cooling time, recorded with a data logger (CR-7, Campbell Scientific) and corrected for potential temperature gradients between soil and psychrometer according to Brown and Bartos (1982). Before placement in the field, psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown and Bartos (1982).

### Leaf water potential and stomatal conductance

Leaf water potential of three covered (non-transpiring) and three exposed leaves on each of two individuals per species was measured with a pressure chamber (PMS Instruments, Corvallis, OR) every 2 h throughout a 24-h cycle. Covered leaves were enclosed in plastic bags and aluminum foil to minimize transpiration. Because differences in  $\Psi_L$  between individuals of the same species were not statistically significant, data for both individuals were pooled. Stomatal conductance of 10 recently mature leaves of a single individual of each species was measured every 2 h throughout a 24-h cycle with a steady state porometer (Model LJ-1600, Li-Cor, Lincoln, NE).

### Sap flow

Sap flow in the main stem of the three species was measured with a heat pulse system based on the work of Marshall (1958), Burgess et al. (1998) and Scholz et al. (2002). A 6-s pulse of heat was produced by applying a known voltage across a 38- $\Omega$  line heater fitted inside a 10- $\mu$ l glass micropipette and inserted in a hypodermic needle. The resulting increase in temperature was measured with 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 cables 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 stems using a template to minimize spacing errors. The heat pulse velocity ( $V_h$ ) was calculated according to Marshall (1958) as:

$$V_h = D_t / x \ln(v_1/v_2) \quad (1)$$

where  $D_t$  is the thermal diffusivity of wet wood,  $x$  is the distance between the heat source (line heater) and the temperature sensors, and  $v_1$  and  $v_2$  are the increases 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  $v_1$  to  $v_2$  was most stable (Burgess et al. 2001). Details of estimates of thermal diffusivity and other parameters and correction factors necessary for sap flow calculations can be found in Burgess et al. (2001) and Scholz et al. (2002). Heat pulses were applied every 30 min. after xylem temperatures around the temperature probes returned to ambient. Sap flow toward the leaves was considered positive and flow toward the roots negative.

Volumetric sap flux ( $V_{sf}$ ) through the stem was obtained by multiplying  $V_h$  by the sapwood cross-sectional area. The active xylem area for water transport was determined by injecting indigo carmine dye near the location where sap flow was measured (Meinzer et al. 1999, 2001). The cross-sectional area of active xylem was highest for *S. ferrugineus* (3.14 cm<sup>2</sup>) and lowest for *O. montana* (2.67 cm<sup>2</sup>). Sap flow was measured on the main stem near the first branching on each plant at 20 to 40 cm below the leaves. Stem diameters were measured with calipers. The stems were thermally insulated in the vicinity of the probes after installation. Some plants were experimentally manipulated by covering them with opaque plastic bags to minimize transpirational water loss. Six to 10 large bags were used to cover the whole plant, depending on the species. Individual branches were covered; however, it was difficult to prevent daytime transpirational water loss completely. 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 the stem section containing the probes, thereby isolating it from the rest of the plant.

### Diurnal variations in stem diameter

Electronic dendrometers (Models DEX70 and DEX100, Dynamax, Houston, TX) were installed near the base of the main stem on the same plants used to measure  $g_s$  and sap flow. Data were obtained every 10 s, and 10-min means were recorded with a datalogger (CR10X, Campbell Scientific), taking the signals from a full-bridge strain gauge attached to a flexible frame of the caliper-style device. The bark was smoothed before attaching the dendrometers to the stems and then covered with rubber foam and aluminum foil to avoid heating by direct solar radiation. The frame temperature was measured with copper-constantan thermocouples to correct for the effect of temperature on the expansion of the frame. To estimate the temperature correction factor, dendrometers were also installed on cut stems with the ends sealed and the whole stem wrapped in aluminum foil to prevent water loss. These stem sections with dendrometers were placed next to the dendrometers used on intact stems to insure similar temperature and light conditions. The temperature correction was 0.046 mm per 20 °C, similar to the temperature correction specified by the manufacturer.

### Results

During two typical days at the end of the dry season,  $D$  remained relatively high throughout the night, indicating that the driving force for nocturnal transpiration was substantial (Figure 1). The value of  $\Psi_s$  was about -1.4 MPa at a soil depth of

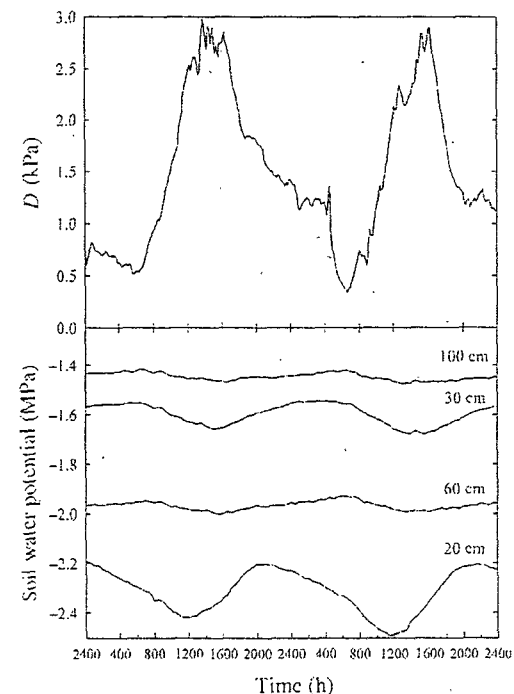


Figure 1. Daily courses of air saturation deficit ( $D$ ) and soil water potential at soil depths of 20, 30, 60 and 100 cm on August 30 and 31, 2002.

100 cm and ranged between  $-2.2$  and  $-2.4$  MPa at 20 cm. The  $\Psi_s$  at 30 cm increased overnight, consistent with the occurrence of hydraulic lift (Scholz et al. 2002). Soil water potential was more negative at 60 cm than at 30 cm, probably reflecting the different patterns of water uptake by the relatively shallow root systems of herbaceous plants and the abundant superficial roots of trees with dimorphic root systems. Evaporation may have contributed to the negative water potential values of the upper soil layer.

The water potential of covered (non-transpiring) leaves was less negative than that of exposed leaves throughout the day in all species studied (Figure 2). The largest differences in  $\Psi_L$  between covered and exposed leaves were observed at about 1400 h concurrent with the highest  $D$  (Figure 1). The difference between covered and exposed  $\Psi_L$  at 1400 h ranged from 0.7 MPa in *R. montana* to about 1.0 MPa in *S. ferrugineus*. At night, differences between exposed and covered  $\Psi_L$  were smaller, ranging from 0 to 0.5 MPa. Values of nighttime  $\Psi_L$  for

both exposed and covered leaves were substantially more positive than the soil water potentials at 100 cm (Figure 1), indicating that the roots were tapping water from depths greater than 100 cm (Jackson et al. 1999). During the wet season also,  $\Psi_L$  of covered leaves was less negative than that of exposed leaves throughout the day (Figure 3). However, predawn  $\Psi_L$  of both covered and exposed leaves was more positive, and the difference between  $\Psi_L$  of covered and exposed leaves was substantially smaller than that during the dry season; although, minimum  $\Psi_L$  of exposed leaves was similar during the wet and dry seasons (Figures 2 and 3).

Stomatal conductance reached maximum values during the morning in all species, and declined more or less continuously until nightfall (Figure 4). However,  $g_s$  never dropped below  $40 \text{ mmol m}^{-2} \text{ s}^{-1}$  at night in any of the three species, and in some cases, rose to as much as  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$  by the end of the dark period. Nocturnal  $g_s$  decreased with increasing  $D$  (Figure 5). The slopes of the relationship, an index of the sensitivity of nocturnal  $g_s$  to variations in  $D$ , were steeper for *S. ferrugineus* and *R. montana* than for *O. hexasperma*. The difference in sensitivity of  $g_s$  to  $D$  between the first two species and *O. hexasperma* was significant at  $P = 0.1$ . The diurnal changes in  $D$  and air temperature during the measurement period were typical of the dry season. Sap flow exhibited diurnal fluctuations typical of those for freely transpiring Cerrado woody plants (Figure 6). Sap flow remained positive at night, particularly on the night of September 2 when  $D$  did not drop below 1 kPa. Sap flow tended to decrease toward the end of the dark period in all species, particularly during the first two nights. Maximum rate of sap flow was about  $40 \text{ cm}^3 \text{ h}^{-1}$  in *S. ferrugineus* and 15 to  $20 \text{ cm}^3 \text{ h}^{-1}$  in the other two species. *Styrax ferrugineus* individuals whose sap flow was measured had a larger leaf surface area and cross section of active xylem at the base of the main stem than *O. hexasperma* and *R. montana*. Covering the trees (Figure 6 arrows) reduced the maximum flow rate, the magnitude of the diurnal fluctuations and the magnitude of nighttime sap flow. In covered plants of *R. montana*, sap flow was negative at night, rapidly became positive soon after sunrise, and began to reverse direction again shortly after midday. The mean volumetric sap flux at night of *R. montana* was about  $-0.6 \text{ cm}^3 \text{ h}^{-1}$  and was only  $-0.25 \text{ cm}^3 \text{ h}^{-1}$  for *O. hexasperma*. Even though the trees were covered with several plastic bags, it was difficult to seal the bags well enough to completely avoid daytime transpirational losses. Consequently, during the period that the trees were covered, they still exhibited daytime water flow, but at a lower rate (Figure 6).

Water potential of freely transpiring leaves decreased linearly with increasing sap flow during the dry season (Figure 7). The  $\Psi_L$  versus sap flow relationships were extrapolated to zero flow to obtain an estimate of  $\Psi_s$  (Sperry et al. 2002). These estimated values of  $\Psi_s$  were similar to the predawn  $\Psi_L$  in covered leaves observed for *R. montana* and *O. hexasperma* (Figure 7). *Styrax ferrugineus*, with the least negative  $\Psi_L$  in covered leaves, had the highest  $x$ -intercept, whereas *O. hexasperma*, with the most negative predawn  $\Psi_L$  in covered leaves, had the lowest  $x$ -intercept.

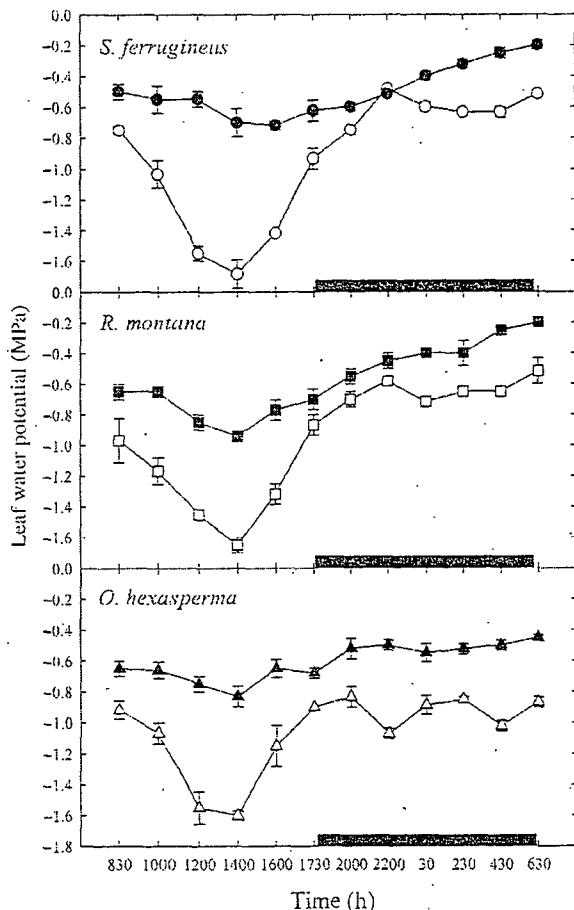


Figure 2. Daily courses of water potential of exposed (open symbols) and covered leaves (closed symbols) during the dry season. Data represent the mean value ( $\pm$  SE) for six leaves. Measurements were obtained on August 30 and 31, 2002. The horizontal bar in each panel indicates the dark period. Air saturation deficit during the measurement period is shown in Figure 1.

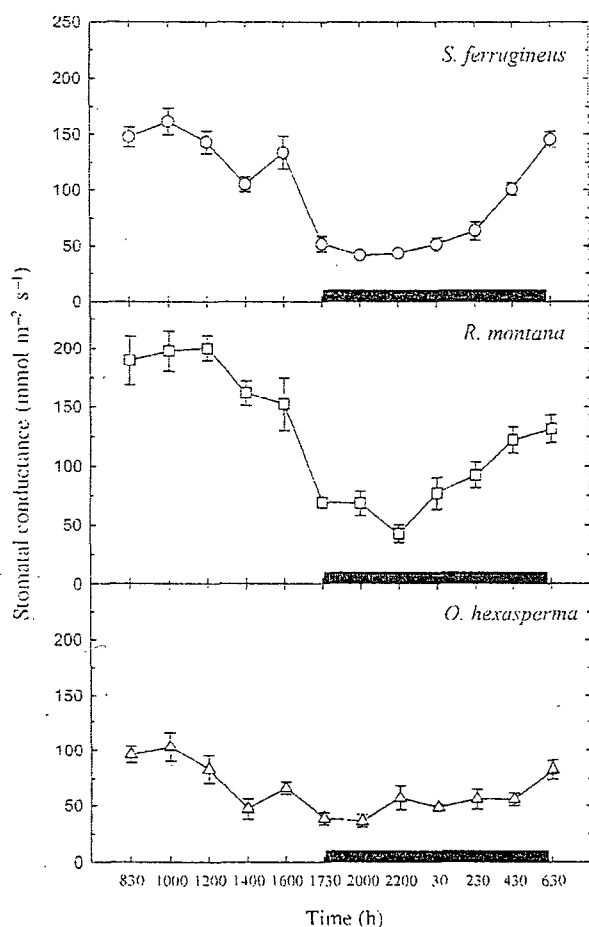


Figure 4. Daily courses of stomatal conductance during the dry season. Data are mean values ( $\pm$  SE) for 10 leaves of a single individual per species. Measurements were obtained on August 30 and 31, 2002. The horizontal bar in each panel indicates the dark period. Air saturation deficit during the measurement period is shown in Figure 1.

Diurnal variations in stem diameter were monitored in freely transpiring individuals of the three woody species (Figure 8). The stem diameter was smallest around midday, consistent with higher sap flows, and tended to increase at night in all three species. The range of diel diameter variations was larger in *S. ferrugineus* and *O. hexasperma* (about 250  $\mu$ m) and smaller in *R. montana* (about 50  $\mu$ m). Different y-axis scales were used for each species to augment the diurnal range of diameter variations. Dendrometers were installed near the base of the main stem at 30 to 50 cm from the soil surface. The stem diameters for each species were: 4.6 cm for *R. montana*, 4.7 cm for *S. ferrugineus* and 4.5 cm for *O. hexasperma*. After covering the trees to minimize transpiration, the stem diameters tended to increase substantially with respect to the initial value and the magnitude of the diurnal fluctuations was reduced, particularly in *O. hexasperma*. Figure 9 depicts nocturnal time courses of stem diameter in the same three species before and immediately after the trees were covered (see Fig-

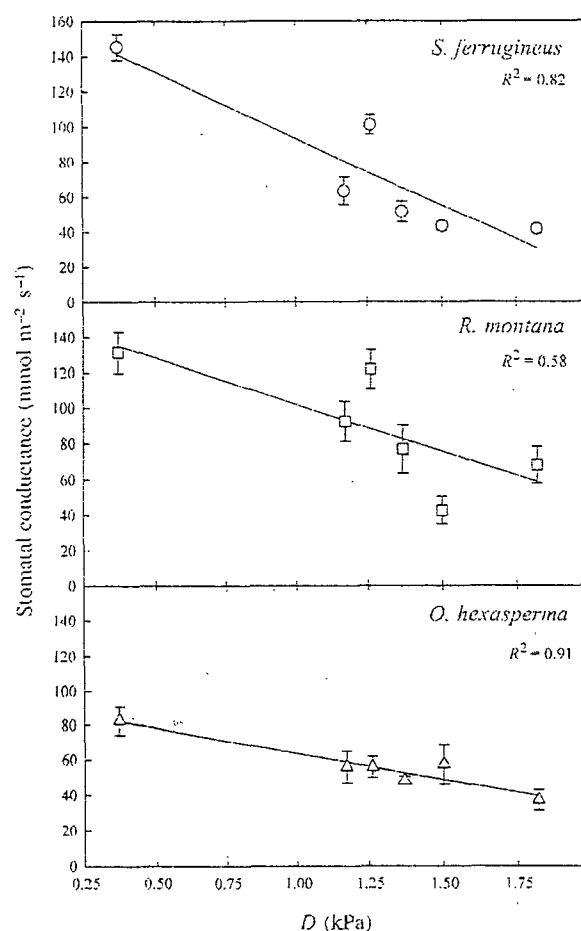


Figure 5. Relationship between nighttime stomatal conductance and air saturation deficit ( $D$ ). Data are mean values ( $\pm$  SE) for 10 leaves of a single individual per species. Measurements were obtained from 2000 h on August 30 till 0600 h on August 31, 2002. The lines are linear regressions fitted to data.

ure 8). In all species, the stem diameter increased more rapidly during the night in covered trees compared with freely transpiring trees, suggesting that the internal water storage compartments tended to recharge faster when nocturnal transpiration was reduced. In *S. ferrugineus*, water was withdrawn from storage after midnight before covering. The mean rates of stem recharge, as indicated by stem diameter increases (positive values) or water withdrawal (negative values), from midnight to 0600 h for four consecutive days before covering, were  $-6.1 \pm 1.6 \mu\text{m h}^{-1}$  for *S. ferrugineus*,  $1.9 \pm 0.9 \mu\text{m h}^{-1}$  for *R. montana* and  $12.4 \pm 1.6 \mu\text{m h}^{-1}$  for *O. hexasperma*.

## Discussion

During the dry season, predawn  $\Psi$  of exposed leaves was about 0.4 MPa more negative than predawn  $\Psi$  of covered leaves, suggesting that Cerrado plants do not achieve internal water potential equilibrium by dawn during this period. These re-

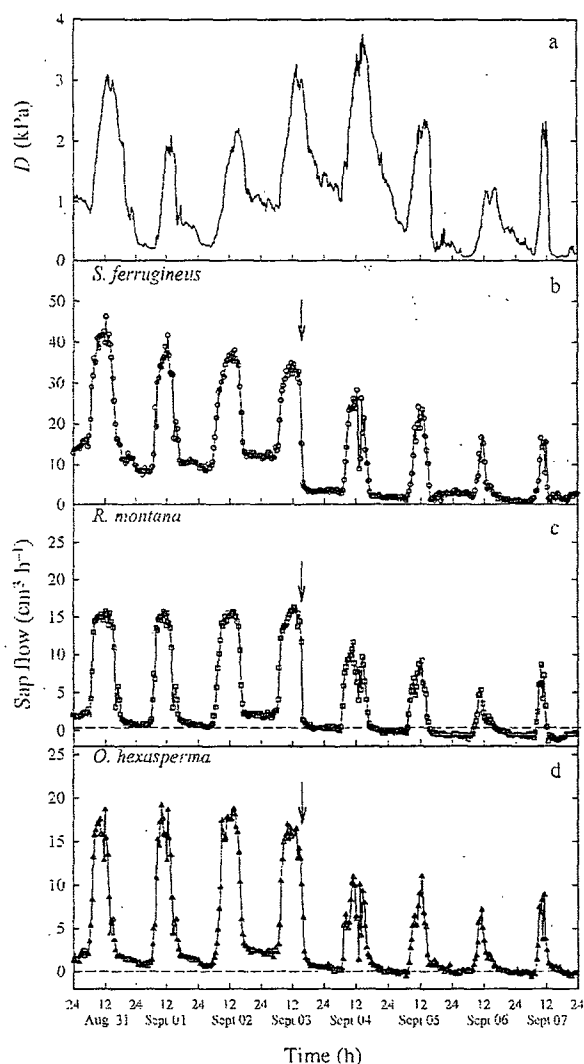


Figure 6. Daily courses of air saturation deficit ( $D$ ) and sap flow in stems between August 31 and September 7, 2002. On September 3, 2002 (down arrows) the plants were covered with opaque plastic bags to restrict transpiration.

sults also suggest that the leaves were somewhat hydraulically isolated because  $\Psi_L$  of covered leaves was substantially higher than that of transpiring leaves of the same individual. A large portion of the liquid-phase resistance in the water transport pathway lies in small twigs, petioles and the leaf lamina itself (Brodribb and Holbrook 2003, Bucci et al. 2003). The  $\Psi_L$  of covered leaves gives an estimate of the water potential of the stem at the point of leaf insertion (Begg and Turner 1970). If the magnitude of nighttime transpiration and hydraulic resistance between the stem and the soil are relatively high, then the predawn  $\Psi_L$  of covered leaves will not provide a good estimate of  $\Psi_s$ . A comparison of this and other approaches for estimating  $\Psi_s$  is provided below. During the wet season, the difference in predawn  $\Psi_L$  of exposed and freely transpiring leaves ranged from 0.2 MPa in *S. ferrugineus* to 0 MPa in *O. hexa-*

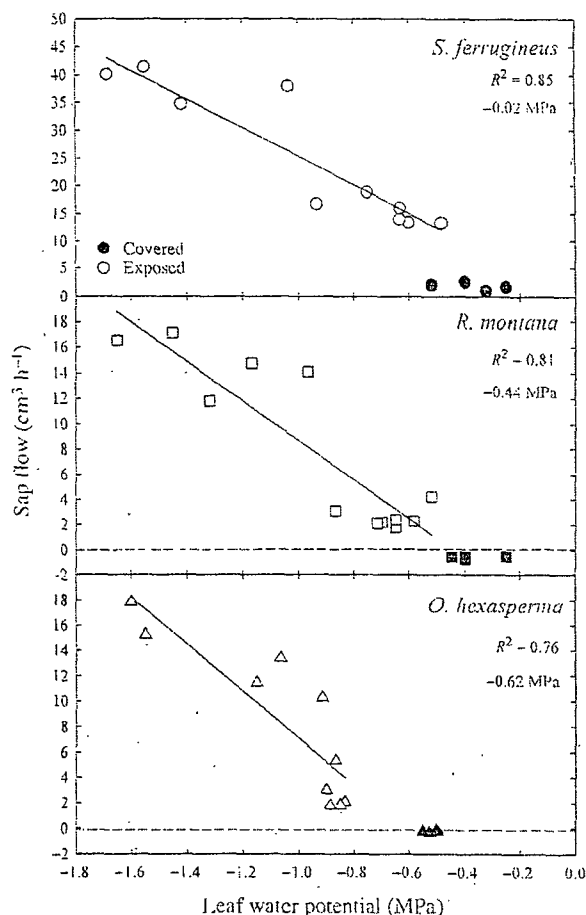


Figure 7. Relationships between sap flow and leaf water potential during the dry season. Open symbols represent values obtained for exposed leaves, and closed symbols represent predawn values for covered leaves. Each value represents the mean sap flow rate and leaf water potential for three individuals per species at different times during August 30 and 31, 2002. The lines are linear regressions fitted to data for exposed leaves. The x-intercept values (predicted leaf water potential at zero flow) are included in each panel.

*sperma*, indicating that even in the wet season,  $\Psi_L$  of some Cerrado plants does not reach complete internal water potential equilibration by dawn.

Cerrado soils usually exhibit strong vertical gradients in  $\Psi_s$  during the dry season (Franco 1998). Horizontal variation in  $\Psi_s$  is usually less pronounced than vertical variation but could still be substantial depending on soil heterogeneity and root activity. Root systems explore these heterogeneous systems and individual roots may be exposed to different soil water potentials. This is particularly evident during the dry season in some savanna woody species with dimorphic root systems. The shallow lateral roots tend to explore soil layers relatively depleted of water, whereas tap roots use water from deeper and wetter soil layers (Sarmiento et al. 1985). Species-specific estimates of the  $\Psi_s$  of soil explored by the roots of each species were obtained by extrapolating the trajectory of sap flow ver-

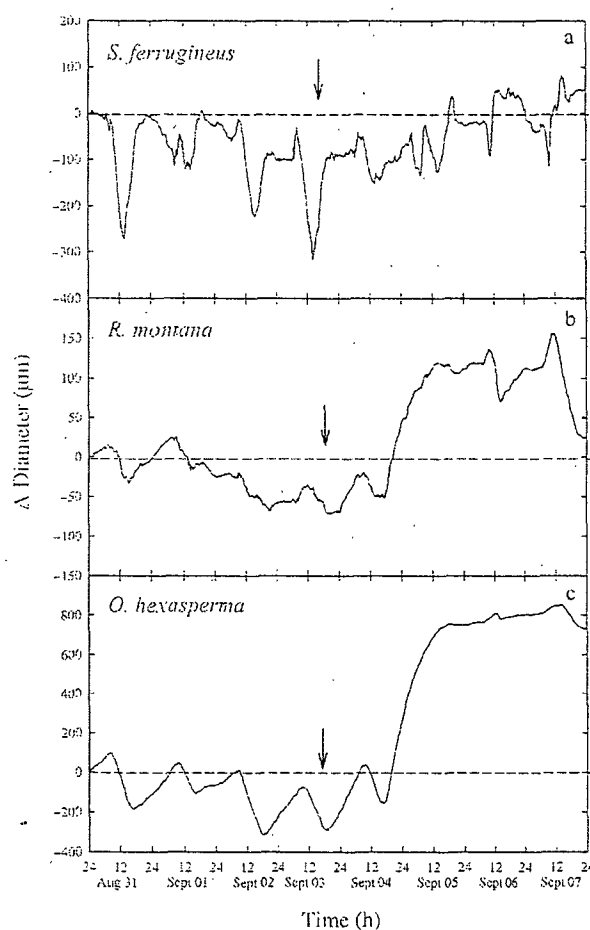


Figure 8. Diurnal changes in stem diameter ( $\Delta$  Diameter referenced to midnight of August 30, 2002) between August 31 and September 7, 2002. On September 3, 2002 (arrow), the plants were covered with opaque plastic bags to restrict transpiration.

sus  $\Psi_L$  relationships to zero flow (Figure 7). This procedure requires that  $\Psi_s$  remains relatively constant when sap flow increases (Sperry et al. 2002). At zero flow,  $\Psi_L$  should equilibrate with the weighted mean  $\Psi_s$  through the portions of the soil profile explored by roots, using as weights the area-specific root and soil resistance and the fine root surface areas in each soil layer. Persistent disequilibrium between  $\Psi_L$  and  $\Psi_s$  in non-transpiring potted plants growing in soil with  $\Psi_s$  uniformly near zero has been attributed to high concentrations of apoplastic solutes in leaf intercellular spaces (Orcival and Berger 1995, Donovan et al. 1999).

In our study, the predicted values of weighted mean  $\Psi_s$ , calculated as the extrapolation to the  $x$ -axis (zero flow) of the linear relationships between sap flow and  $\Psi_L$ , were similar to predawn  $\Psi_L$  of covered leaves for two of the species and substantially more positive than the measured predawn  $\Psi_L$  of exposed leaves in *S. ferrugineus*. For example, the  $\Psi_s$  predicted from the sap flow versus  $\Psi_L$  relationship for *R. montana* was  $-0.44$  MPa and nighttime  $\Psi_L$  of covered leaves in the same species was  $-0.45$  to  $-0.25$  MPa. Predawn  $\Psi_L$  of exposed

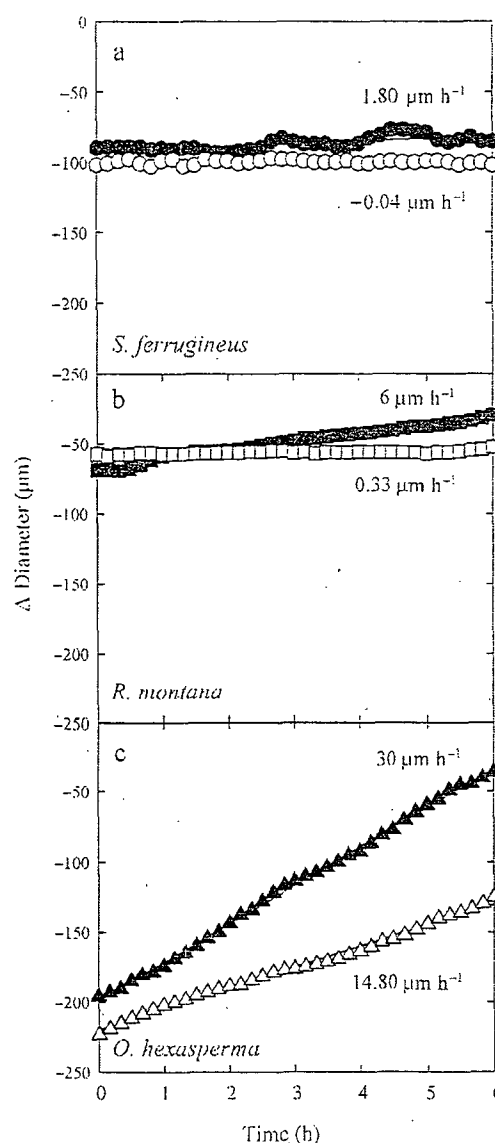


Figure 9. Stem diameter changes ( $\Delta$  Diameter) from midnight to 0600 h for exposed trees (open symbols) and covered trees (filled symbols) on September 3 and 4, 2002, respectively. The plants were covered with opaque plastic bags during the afternoon of September 3, 2002, to restrict transpiration. The mean rates of diameter increase or decrease are also shown.

leaves for the same species was  $-0.7$  MPa. The predicted  $\Psi_s$  was  $0.2$  MPa greater than the  $\Psi_L$  of covered leaves in *S. ferrugineus* and only  $0.05$  MPa lower in *O. hexasperma*.

The relatively high nocturnal sap flows in *S. ferrugineus* may have contributed to the  $0.2$  MPa difference between the predicted  $\Psi_s$  and the  $\Psi_L$  of covered leaves (Begg and Turner 1970). The magnitude of predawn water potential disequilibrium between leaves and soil in our study was consistent with previous reports in the literature for Chaparral shrub species and temperate trees such as *Pinus palustris* Mill. (Donovan et al. 1999). Predawn disequilibrium in warm desert woody

plants such as *Larrea tridentata* (DC.) Cov., on the other hand, is about 1.0 MPa (Meinzer et al. 1988).

Nocturnal transpiration, measured with heat pulse probes, was relatively high in the study species and constituted from 13 to 28% of total daily transpiration. Consistent with these nocturnal transpiration rates,  $g_s$  remained relatively high during the night, and in some cases reaching values as high as  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ . Although  $g_s$  decreased with increasing  $D$  at night, responses of nocturnal transpiration depended on the magnitude of decreasing  $g_s$  relative to increase in  $D$ . In *S. ferrugineus* and *R. montana*, it appeared that decreases in  $D$  toward the end of the nighttime period compensated for increases in  $g_s$ , resulting in similar levels of sap flow throughout the night.

In non-transpiring plants, several factors may contribute to the failure of  $\Psi_L$  to reach equilibrium with  $\Psi_s$  before dawn. Donovan et al. (1999) found that the  $\Psi_L$  of covered leaves reached equilibration with  $\Psi_s$  several hours before dawn. In our study,  $\Psi_L$  of covered leaves did not stabilize in any of the plants before the end of the dark period, indicating that the duration of the night was insufficient to allow leaf–soil water potential equilibration. In *S. ferrugineus* and *R. montana*, for example, covered leaf  $\Psi_L$  increased at a constant rate of 0.05 MPa per hour from about 0200 to 0600 h. At least two mechanisms may have prevented overnight equilibration between leaf and soil water potential in non-transpiring plants of the Cerrado woody species studied. One potential mechanism is the time needed for the recharge of the large elastic and inelastic stem water storage compartments. There are two types of water storage compartments in stems of Cerrado plants: those associated with the xylem tissue, particularly the sapwood, and those associated with the parenchyma tissue of the bark that comprise more than 24% of the stem tissue in many species (Coradin 2000). Diurnal changes in stem diameter were taken in this study as a proxy for the dynamics of water movement during utilization and recharge of stem water. Diurnal changes in stem parenchyma and xylem tissue water content were consistent with the expansions and contractions of stems during 24-h cycles (results not shown). Stem water stores tended to recharge faster when nocturnal transpiration was reduced, suggesting that freely transpiring individuals were either using water from internal stem stores before dawn or that water that could be used to recharge stem storage compartments was used to compensate nocturnal transpirational water losses. Incomplete recharge of internal water storage may explain the steady increase in  $\Psi_L$  of covered plants at night and the failure to achieve complete equilibration even when nocturnal transpiration was largely prevented.

Another potential mechanism that could have prevented overnight leaf–soil water potential equilibration in non-transpiring plants is hydraulic redistribution, the movement of water from wetter to drier regions of the soil profile via plant roots (Scholz et al. 2002). Hydraulic redistribution may occur when  $\Psi_s$  of the soil around shallow roots is lower than stem water potential. Soil water potentials in the  $-1.5$  to  $-2.5$  MPa range were frequently observed in the upper soil layers during the dry season in Cerrado ecosystems (Figure 1). Consequently, soil near shallow roots can constitute a competing sink for water taken up by deep roots that could otherwise re-

place water lost from the leaves at night or be used for water storage recharge. During the dry season, hydraulic redistribution is a common phenomenon in Cerrado woody plants with dimorphic root systems (Scholz et al. 2002, Moreira et al. 2003). Shallow roots of some Cerrado species exhibit positive sap flow during the day, but negative sap flow during the night. In other species, shallow roots exhibit negative sap flow during both the day and night, indicating that hydraulic redistribution occurs continuously (Scholz et al. 2002). Even though reverse flow commonly occurs in roots of Cerrado species, the significance of hydraulic redistribution for the overall water economy of the plants is still debatable (Moreira et al. 2003). It is puzzling that, in our study, sap flow was negative at night in the stems of some covered plants, particularly in those individuals whose water storage recharge was still incomplete by the end of the night. It is possible that the water that condensed on the expanding and recently expanded leaves of the bagged plants at night was absorbed by the leaves, resulting in partial recharge of internal water storage tissues and downward movement of water into the shallow roots, most of which occurred in relatively dry soil layers.

This study showed that nighttime transpiration and recharge of internal water storage compartments are two important processes contributing to predawn disequilibrium between  $\Psi_L$  and  $\Psi_s$  in Cerrado plants. Stomata responded to variations in  $D$  at night, and nocturnal variation in sap flow was consistent with species-specific differences in nocturnal sensitivity of  $g_s$  to changes in  $D$ . The pattern of sap flow was also consistent with the expansion and contraction of stems, and therefore with the dynamics of water movement during utilization and recharge of stored water.

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