Controls on stand transpiration and soil water utilization along a tree density gradient in a Neotropical savanna

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ABSTRACT

Environmental controls of stand-level tree transpiration (E) and seasonal patterns of soil water utilization were studied in five central Brazilian savanna (Cerrado) sites differing in tree density. Tree density of Cerrado vegetation in the study area consistently changes along topographic gradients from ∼1000 trees ha^{-1} in open savannas (campo sujo) at the lower end of the topographic gradient to >3000 trees ha^{-1} in woodlands (cerradão) at the upper end of the gradient. Tree canopy resistance (r_C) increased linearly with increasing daily mean air saturation deficit (D) at all sites, but cerradão and cerrado denso sites with higher tree density and higher tree leaf area index (LAI) had lower r_C values at all values of D compared to physiognomies with lower tree density, suggesting that r_C was less sensitive to changes in D in physiognomies with high tree density and LAI. During the peak of the dry season, mean soil water potential at 0.20 m depth was most negative in the sites with the lowest tree basal area and increased linearly with basal area across sites. In contrast, soil water storage in the 0.10–2.50 m layer decreased exponentially with increasing basal area, consistent with trees in higher density sites utilizing a larger proportion of available soil water at depth during the dry season. Maximum tree transpiration was highest in the cerradão and cerrado denso (∼0.81 mm day^{-1}). Despite higher evaporative demand during the dry season, E was similar between the dry and wet seasons within each study site, which was associated with lower LAI and canopy conductance (g_C) during the dry season compared to the wet season. Leaf area index was a good predictor of E and g_C. For both dry and wet season data combined, E increased asymptotically with increasing LAI across all physiognomic types, allowing LAI to be used as a predictor of spatial variation of E. The lack of seasonality in E across the Cerrado physiognomies studied could not be explained by

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individual constraining variables such as D or soil water potential near the surface, but was consistent with the influence of multiple regulatory effects of D and soil water potential on seasonal changes in leaf area and g_C.

1. Introduction

Natural vegetation is usually composed of a mixture of many species, each having different responses to variations in environmental conditions and driving forces, making it difficult to predict ecosystem mass and energy exchange based on measurements at the individual plant level. For example, responses to soil drying in ecosystems with seasonal variation in soil water availability will depend on patterns of root distribution. As the upper soil layers dry, shallow-rooted species may exhibit large reductions in transpiration, while deeply rooted species may exhibit greater stability of transpiration in the face of drying of upper soil layers (Granier and Loustau, 1994; Meinzer et al., 1999; Pataki et al., 2000). The problem becomes more complex if the goal is to predict how transpiration will respond to increasing demands on soil water resources along gradients of vegetation structure.

Estimates of transpiration in trees based on sap flow can be scaled up to the stand level using a variety of approaches (Granier et al., 1996; Oren et al., 1996, 1998; Martin et al., 1997; Kostner et al., 1998). Regardless of the approach, estimates of stand transpiration require accurate measurements of mass flow of sap per tree. This is feasible if sap flux density (J_S) is adequately characterized across the depth of the active xylem and if the dependence of mass flow on tree size is known (Phillips et al., 1996; Kostner et al., 1998; Oren et al., 1998; Ford et al., 2004).

The extremely seasonal environment of Neotropical savanna ecosystems of Central Brazil (Cerrado) is characterized by about five rainless months, and a long period with high precipitation. Evaporative demand is substantially higher during the dry season. The combination of higher evaporative demand and a long dry season makes the Cerrado a potentially stressful environment for woody species. Most woody species in the Cerrado are evergreen with large scleromorphic leaves that are gradually shed during the dry season, but new leaves are produced before the wet season begins. Only a few species are deciduous, but even these remain leafless for only a short period of time during the dry season. Regardless of their pattern of leaf phenology, nearly all Cerrado species exhibit reductions in leaf surface area during the dry season when taking into account the average leaf surface area for the entire season (Bucci et al., 2005).

The savannas of central Brazil show consistent changes in tree density along shallow topographic gradients of several hundred meters in length. Vegetation structure varies from open savannas with relatively few trees in the lower portions of the topographic gradient (campo sujo) to woodlands with a relatively high density of trees in the upper portions of the gradient (cerradão). Herbaceous plant abundance follows the opposite trend, with higher coverage in open savannas to very low coverage in closed savannas (Hoffmann et al., 2005). This is an ideal model system for understanding the effects of changes in water resource availability and canopy conductance on transpiration along a gradient of increasing tree density. The main objective of the present study was to characterize environmental and physiological controls on seasonal patterns of stand-level tree transpiration along a tree density gradient in the Brazilian Cerrado. We measured sap flow and leaf area index (LAI) in dominant tree species, soil water potential and volumetric water content at several depths, air temperature and relative humidity, and rainfall during wet and dry seasons in five representative Cerrado physiognomies differing in tree density. Data on photosynthetic photon flux density (PPFD) were obtained for only two of the sites but this information was not included in this study because it was assumed that PPFD is not an important controlling variable for explaining changes in water utilization by woody species along the gradient where LAI in most stands is low.

2. Materials and methods

2.1. Study site

The study was carried out at the Instituto Brasileiro de Geografia e Estatistica (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasilia, Brazil (lat. 15°56′, lon. 47°53′W, alt. 1100 m). The IBGE includes extensive areas of all major physiognomies of Cerrado vegetation from very open to closed savannas. Annual precipitation in the reserve ranges from 880 to 2150 mm with a mean of approximately 1500 mm. There is a pronounced dry season from May through September with the months of June, July and August being nearly rainless. Mean annual temperature is about 22 °C, with little seasonality. Maximum diurnal air temperature differences, on the other hand, can be as large as 20 °C during a typical dry season day. The soils are very deep oxisols with a high percentage of clay. Despite their high clay content, the soils behave like coarser-textured soils and are extremely well drained.

Field measurements were made between April 2002 and March 2003. Five physiognomies along a gradient of increasing tree density were selected: campo sujo, campo cerrado, cerrado sensu stricto, cerrado denso and cerradão. Campo sujo is an open savanna with scattered shrubs and few trees, campo cerrado is an open savanna with shrubs and trees in similar proportion, cerrado sensu stricto is a tree savanna, cerrado denso is a dense tree savanna, and cerradão is a nearly closed-canopy savanna, or woodland. A total of 24 tree species were selected for this study based on their phenology and abundance in Cerrado vegetation. Several of these tree species spanned all or a large portion of the entire gradient. The most important families in terms of species and abundance are Leguminosae, Malpighiaceae, Myrtaceae, Melastomataceae and Rubiaceae (Heringer et al., 1977). The frequency

distributions of tree diameters were roughly similar in all physiognomies with the largest numbers of individuals in the smaller class sizes and decreasing exponentially at larger diameters. The cerradão and the cerrado denso, the two physiognomies with the highest tree density, had more individuals in the largest two size classes (larger than 14 cm DBH) compared to the other three physiognomies. Mean basal area (cm^2) per tree larger than 1-m-tall and 4 cm DBH were: 46 ± 5 (campo sujo); 25 ± 2 (campo cerrado); 39 ± 3; 62 ± 7 (cerrado denso); and 80 ± 17 (cerradão).

Analyses of soil physical properties were made on four soil samples per site and were performed by the soil laboratory of the Agricultural Research Center for the Cerrado region (EMBRAPA, Brazil). The soils along the gradient had similar bulk density (990 ± 20 kg m^{-3}), macro porosity ($17.9 \pm 0.4\%$) and texture fraction (silt/clay, 0.22 ± 0.02) at 10, 20, 30, 60 and 100 cm depth. Field capacity and micro-porosity at 30, 60 and 100 cm depth were significantly lower in the campo sujo site than in the other physiognomies ($P < 0.1$). Mean field capacity (%) of the 30–100 cm soil layer was 38 in the campo sujo, and ranged from 41 to 43 in the other Cerrado physiognomies.

2.2. Sap flow

Sap flow was measured in trees of 24 species ranging from evergreen to brevideciduous and deciduous and with the highest importance value indices (Felfili et al., 1994). Measurements were obtained during 6–8 months throughout the year to have a good representation of sap flow behavior during dry and wet season periods (several days per month and 3–4

months during the dry and 3–4 months during the wet seasons). The species studied, their leaf phenology, the numbers of individuals studied, site type where each species was studied, and the mean stem diameters are listed in Table 1. The heat dissipation method (Granier, 1985, 1987) was used for sap flow measurements. A pair of 20-mm long, 2-mm diameter hypodermic needles, which contain a copper-constantan thermocouple inside a glass capillary tube and a heating element of constantan coiled around the tube, were inserted into the sapwood near the base of the main stem in each plant (22–24 trees in each site). The upper (downstream) probe was continuously heated at a constant power by the Joule effect, while the unheated upstream probe served as a temperature reference. Temperature differences between the upstream and downstream probes were recorded every 10 s and 10-min averages recorded using dataloggers (CR 10X, Campbell Scientific, Logan, Utah, USA).

Sap flux density (J_S) was calculated from the temperature difference between the two probes using an empirical calibration (Granier, 1985, 1987) re-validated for tropical trees (Clearwater et al., 1999; McCulloh et al., 2007). The temperature differences were corrected for natural temperature gradients between the probes (Do and Rocheteau, 2002). Mass flow of sap per individual was obtained by multiplying sap flux density by sapwood cross-sectional area. The relationship between sapwood cross-sectional area and stem diameter was obtained by injecting dye near the base of the main stem for several individuals of each species representing a range of diameters. The r^2 of the linear relationships were higher than 0.73. After 2 h the plants were decapitated a few cm above the point of dye

Table 1 – Species studied and family, leaf phenology, number of individuals per species (n) studied, sites were each species was studied, and mean basal diameter (cm $\pm$ S.E.), for species with $n > 3$

Species	Family	Phenology	n	Sites	Diameter
Byrsonima crassa	Malpighiaceae	BD	12	cs, cc, css, cd, co	7.3 ± 0.4
Blepharocalyx salicifolius	Myrtaceae	BD	8	cc, css, cd, co	15.2 ± 3.6
Caryocar brasiliense	Caryocaraceae	BD	5	css, cd	8.6 ± 1.6
Guapira noxia	Nyctaginaceae	BD	4	cs, cc, css, co	7.6 ± 1.0
Dalbergia miscolobium	Leguminosae	BD	11	cs, cc, css, cd, co	7.9 ± 0.4
Davilla elliptica	Dillenaceae	BD	3	cs, cc, css	7.3 ± 1.8
Eremanthus glomerulatum	Compositae	E	2	cs, cc	5.2
Eriotheca pubescens	Bombacaceae	BD	5	cs, cc, css	9.9 ± 1.6
Erythroxylum suberosum	Erythroxylaceae	BD	2	cs, css	5.3
Kielmeyera coriacea	Guttiferae	D	6	cs, cc, css, co	5.7 ± 0.4
Miconia ferruginata	Melastomataceae	E	1	cd	8.7
Myrsine guianensis	Myrsinaceae	E	2	cc, co	5.8
Ouratea hexasperma	Ochnaceae	E	2	css	5.5
Pouteria ramiflora	Sapotaceae	BD	2	cs	5.3
Pterodon pubescens	Leguminosae	E	4	css, cd, co	7.7 ± 0.8
Qualea grandiflora	Vochysiaceae	D	2	cd, co	8.8
Qualea parviflora	Vochysiaceae	D	5	cs, cc, css, cd, co	5.9 ± 0.9
Roupala montana	Proteaceae	E	7	cs, cc, css,	5.8 ± 0.8
Schefflera macrocarpa	Araliaceae	E	11	cs, css, cd, co	8.7 ± 0.9
Sclerolobium paniculatum	Leguminosae	E	5	css, cd	14.9 ± 1.7
Stryphnodendron adstrinens	Leguminosae	BD	3	cs, cc	7.1 ± 0.5
Styrax ferrugineus	Styracaceae	E	10	cs, cc, css, cd	8.9 ± 0.7
Vochysia elliptica	Vochysiaceae	E	1	cd	6.8
Vochysia thyrsoideae	Vochysiaceae	E	5	cs, cd, co	7.2 ± 0.8

Abbreviations are: BD (brevideciduous); E (evergreen); D (deciduous); cs (campo sujo); cc (campo cerrado); css (cerrado sensu stricto); cd (cerrado denso); co (cerradao).

injection and the area of conducting tissue was determined from the pattern of staining by the dye as it moved in the transpiration stream. The average cross-sectional area of active xylem in all trees studied was 28 cm^2, and the average thickness of the sapwood was 3-cm, indicating that the 20-mm probes used spanned most of the conductive portion of the xylem.

2.3. Stand tree transpiration and canopy conductance

Mass flow of sap per individual was scaled to obtain tree transpiration at the stand level (E, mm day^{-1}) according to the following equation:

$$E = \left(\frac{F}{BA_i}\right) BA_T \tag{1}$$

where F is average daily sap flow per tree (kg day^{-1}) obtained from 3 to 4 days of measurements per month, BA_i is mean basal area per tree (cm^2), and BA_T is total basal area per unit of ground (cm^2 m^{-2}). The total basal area per unit of ground (cm^2 m^{-2}) was estimated in ten 10 m × 20 m plots for each physiognomy with the exception of the cerradão (highest density physiognomy) where only five 10 m × 20 m plots were used. In each plot all individuals larger than 1-m-tall and more than 4-cm DBH were identified and measured. Annual or wet and dry season E are the average of monthly E values.

Canopy conductance to water vapor (g_C; mm s^{-1}) was calculated from average diurnal E (600–1800 h, mm day^{-1}) and average diurnal air saturation deficits (D, kPa), using the equation suggested by Monteith and Unsworth (1990):

$$g_C = K_c(T_A)\frac{E}{D} \tag{2}$$

where K_c is the conductance coefficient (115.8 + 0.4236T_A; kPa m^3 kg^{-1}) which accounts for temperature effects on the psychrometric constant, latent heat of vaporization, specific heat of air at constant pressure and the density of air, and T_A is bulk air temperature (Phillips and Oren, 1998). Canopy resistance (r_C; s mm^{-1}) was obtained as the inverse of g_C. Phillips and Oren (1998) showed that errors associated with lumping the temperature-dependent physical coefficients into K_c are negligible. This simplification requires that vertical gradients in D between the leaf surfaces and the bulk air above the canopy be small. Consistent with this, in previous work conducted in the same study region it was found that boundary layer conductance of Cerrado vegetation was high resulting in relatively good aerodynamic coupling between the canopy and the atmosphere (Miranda et al., 1997). The simplification in Eq. (2) also requires that tree water storage above the sap flow measurement point be small. Although Cerrado trees have stems with high capacitance, the discharge and recharge is completed during the daytime (Scholz et al., 2007, in press) making its impact on canopy conductance calculations negligible.

2.4. Leaf area index

Woody species LAI was estimated with a LAI 2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska, USA). In each site 50 locations permitting measurements that included

only tree or shrub canopies were permanently marked, and the measurements were made from these points with a 45° view cap and only during cloudy days or at dawn or dusk. To avoid underestimation of LAI, the measurements were made only under tree canopies at points where the entire angle of view intercepted one or more tree or shrub crowns. To obtain an estimate of stand LAI, the crown LAI values were multiplied by the fraction of ground area covered by tree crowns (Asner et al., 1998). Measurements were made during the wet season (December, February and April) and dry season (June, August and September). To assess the accuracy of LAI estimates performed with the LAI-2000, destructive measurements of LAI for 14 trees and shrubs were done. Crown area was estimated assuming each crown to be an ellipse and by measuring their major and minor axis. Five measurements of LAI were performed under each individual with the LAI 2000. All leaves were collected from the tree, and stem area index (SAI) of the defoliated tree was estimated with the LAI-2000 using the same procedure. The surface area of approximately 30 of leaves was measured with a CI-202 Area Meter (CID Inc., Vancouver, WA, USA) These and the remaining leaves were dried to constant mass at 70 °C and total leaf area per tree determined using the ratio of leaf area to leaf mass obtained from the subsampled leaves. Total leaf area per tree was subsequently converted to LAI dividing leaf area by canopy area. The average LAI/sapwood area ratio was calculated for dry and wet seasons across all physiognomies.

2.5. Soil water potential and water content

Soil psychrometers (PST-55, Wescor, Logan, UT) were used to continuously monitor Ψ_{soil} at 0.20, 0.30, 0.60 and 1.00 m. Before placement in the field, the psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown and Bartos (1982). Soil water potential was measured every 30 min in the psychrometric mode with a 30-s cooling time and data were recorded by a data logger (CR-7, Campbell Scientific, Logan, Utah, USA) and corrected for potential temperature gradients between soil and psychrometer according to Brown and Bartos (1982).
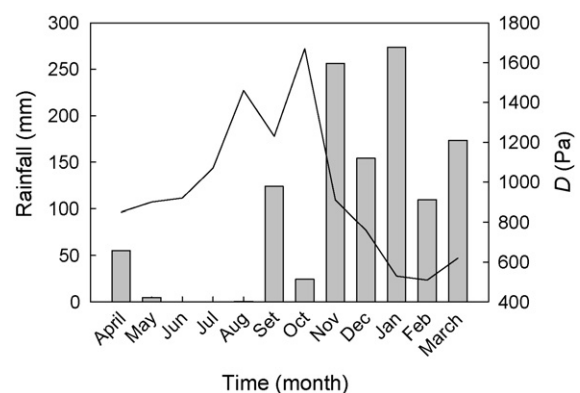

Fig. 1 – Seasonal variations in monthly precipitation and mean air saturation deficit (D) from April 2002 to March 2003 at the IBGE research station. Bars are precipitation and the continuous line is D.
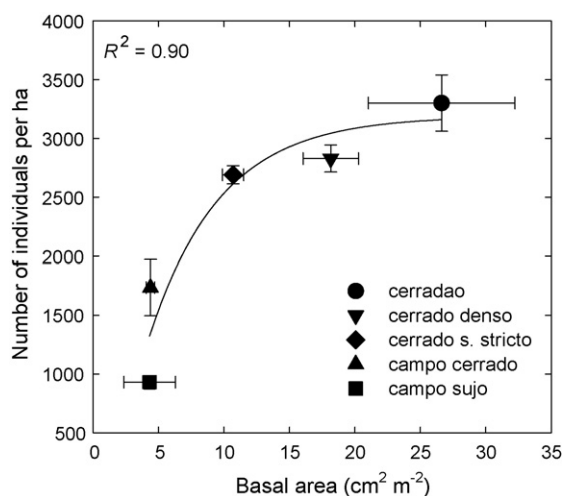
Fig. 2 – Relationship between tree density and stand basal area along the gradient. The function fitted to the data is $y = 3369(1 - \exp(-0.12x))$, $P = 0.016$.

Soil volumetric water content was continuously monitored with multi-sensor frequency domain capacitance probes (Paltineanu and Starr, 1997) at three to four replicate locations per site during 3–4 days each month. The highly sensitive probes contained eight annular capacitance sensors (Sentek PTY Ltd., Adelaide, Australia) positioned at depths of 0.10, 0.20, 0.30, 0.60, 1.00, 1.50, 2.00 and 2.50 m mounted on a single plastic rail and were placed in weatherproof PVC access tubes. All sensors were monitored every 30 min and the measurements stored by a data logger (Model RT6, Sentek). Each sensor was calibrated in the field for the air and water frequency reading endpoint for determination of the normalized frequency. The factory default calibration equation was used. Soil water storage (measured in mm) was calculated by summing the water content for each 0.10-m sensor. When there was a gap between sensors (e.g. 0.30 or 0.60 m), water storage in the intervening layer was interpolated as an average of the sensors above and below the layer summed over the number of 0.10-m intervals in the layer.

2.6. Environmental variables

Air temperature and relative humidity were monitored with humidity probes (HMP35C, Vaisala, Helsinki, Finland) and precipitation was measured with a rain gauge (model TS525, Texas Electronics) in an automated weather station placed at 16 m height near the center of the study area. Values of temperature and humidity were recorded continuously with a datalogger (CR 10X, Campbell Scientific, Logan, Utah, USA). Air saturation deficits (D) were calculated from relative humidity and air temperature measurements.

3. Results

The study period extended from April 2002 to March 2003. The dry season (May through August (Fig. 1) was practically rainless. The air saturation deficit (D) was two- to threefold
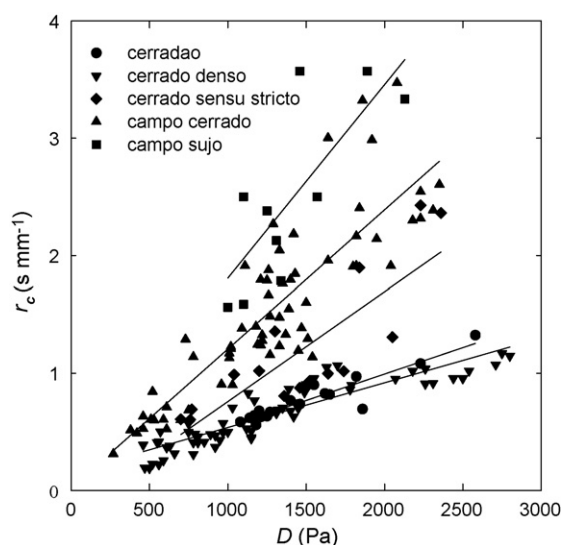

Fig. 3 – Relationship between daily mean canopy resistance (r_C, s mm^{-1}) and daily mean air saturation deficit (D, Pa) during the dry and wet season. Different linear regressions were fitted to the r_C versus D relationships for each physiognomy (cerradão: $y = 93 + 0.45x$, $r^2 = 0.87$, $P < 0.001$; cerrado denso $y = 0.16 + 0.38x$, $r^2 = 0.82$, $P < 0.001$; cerrado sensu stricto: $y = -0.18 + 0.94x$, $r^2 = 0.69$, $P < 0.001$; campo cerrado: $y = 0.021 + 1.18x$, $r^2 = 0.74$, $P < 0.001$; campo sujo: $y = 0.16 + 1.65x$, $r^2 = 0.60$, $P < 0.001$).

greater during the dry season than during the wet season particularly towards the end of the dry season.

Tree density increased asymptotically with increasing stand basal area, from 930 trees ha^{-1} in the campo sujo to
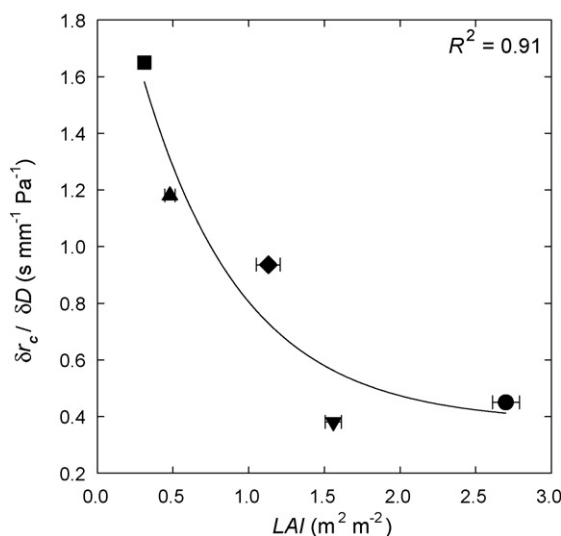

Fig. 4 – Canopy resistance per unit change in vapor pressure deficit ($\delta r_C/\delta D$) as a function of annual mean LAI for all physiognomies along the gradient The line is an exponential decay function fitted to the data $y = 0.4 + 1.9 \exp(-1.5x)$, $P < 0.1$. $\partial r_C/\partial D$ is the slope of the linear relationships obtained between r_C and D as shown in Fig. 3. Symbols as in Fig. 3.
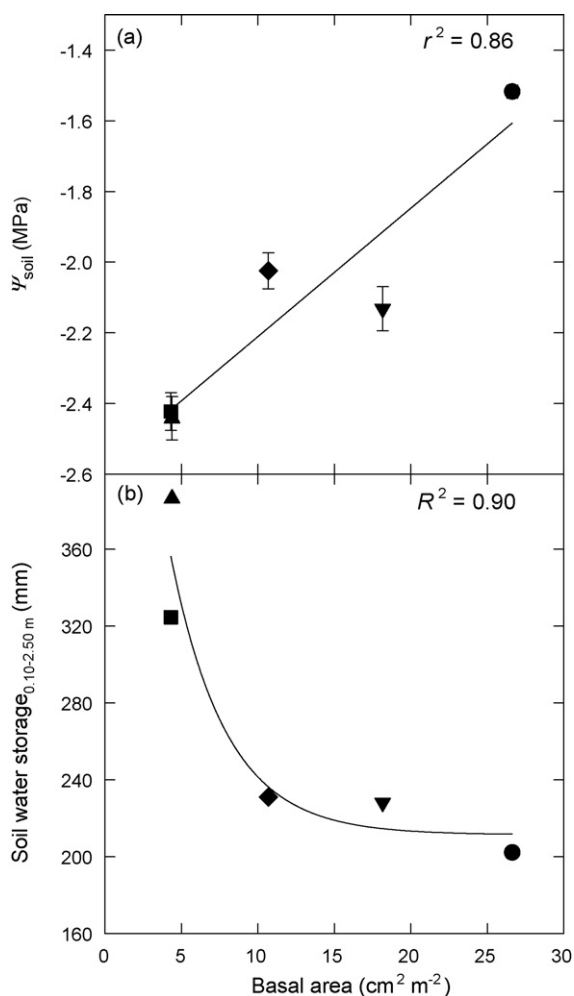
Fig. 5 – Mean soil water potential at 0.20 m depth and soil water storage between 0.10 and 2.50 m depth in relation to total basal area (cm² m⁻²) during the peak of the 2002 dry season (August) in five physiognomies along the gradient. The line in (a) is a linear regression fitted to the data: $y = -2.57 + 0.04x$, $P < 0.05$. The line in (b) is an exponential decay function fitted to the data: $y = 211 + 478 \exp(-0.3x)$, $P < 0.1$. Symbols as in Fig. 3.
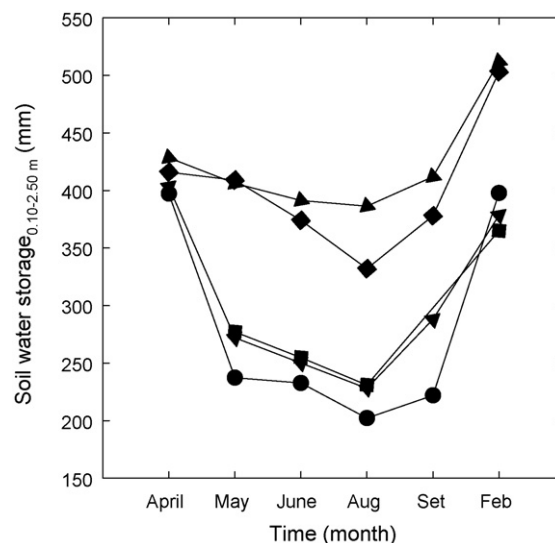

Fig. 6 – Seasonal variation in soil water storage in the 0.10–2.50 m layer in five physiognomies along the gradient. Symbols as in Fig. 3.

Canopy resistance (r_C, mm s⁻¹) increased linearly with increasing mean daily D with the slopes of the r_C versus D relationships tending to decrease as tree density increased (analysis of covariance, $F = 25.656$, $P < 0.05$) (Fig. 3). Cerradão and cerrado denso sites, with the highest tree densities, had lower r_C values at all values of D compared to physiognomies with lower tree density. The sensitivity of r_C to changes in D ($\partial r_C/\partial D$) decreased exponentially with increasing LAI from campo sujo to cerradão (Fig. 4).

Soil water potential (Ψ_{soil}) remained near 0 MPa during most of the wet season (results not shown) and then became more negative as the dry season progressed, particularly in the upper soil layers. During the peak of the dry season (August), Ψ_{soil} became progressively less negative with depth with the exception of the cerradão site (Table 2). The increase in Ψ_{soil} from 0.20 to 1.00 m was more pronounced in sites with lower tree density, with the differences in Ψ_{soil} decreasing from about 1.1 to 1.2 MPa in the campo sujo and campo cerrado sites to 0.68 MPa in the cerrado sensu stricto site to only 0.09 MPa in the cerradão site. Mean Ψ_{soil} at 0.20 m depth during August increased linearly with basal area across the tree density gradient (Fig. 5a). In contrast, total soil water storage between 0.10 and 2.50 m during the same time period decreased

3300 trees ha⁻¹ in the cerradão site (Fig. 2). The frequency distributions of tree diameters were roughly similar in all physiognomies with the largest numbers of individuals in the smaller class sizes (results not shown).

Table 2 – Soil water potentials (Ψ_{soil}) at 0.20, 0.30, 0.60 and 1.00 m depth during the peak of the dry season (August) in five Cerrado physiognomies (means ± 1 S.E.).

Depth (m)	Ψ_{soil} (MPa)				
	Campo sujo	Campo cerrado	Cerrado sensu stricto	Cerrado denso	Cerradão
0.20	−2.43 ± 0.07 a	−2.39 ± 0.32 a	−2.05 ± 0.05 b	−2.14 ± 0.06 b	−1.52 ± 0.02 c
0.30	−2.27 ± 0.09 a	−1.88 ± 0.16 b	−1.89 ± 0.06 b	−1.92 ± 0.16 b	−1.43 ± 0.07 c
0.60	−2.17 ± 0.35 a	−1.97 ± 0.25 a	−1.50 ± 0.06 b	−1.82 ± 0.15 a	−1.64 ± 0.19 a, b
1.00	−1.32 ± 0.24 a, b	−1.21 ± 0.28 a, b	−0.92 ± 0.05 a	−1.46 ± 0.15 b	−1.63 ± 0.10 b

Values followed by the same letter within a row are not significantly different at $P = 0.05$.

exponentially with increasing basal area (Fig. 5b). Soil water storage in the upper 2.50 m was nearly identical across sites at the end of the wet season (April), but reached substantially lower dry season minimum values (August) in the three sites with the highest tree density (Fig. 6).

Despite higher evaporative demand (Fig. 7a) and lower soil water potential during the dry season, stand transpiration (E, mm day^{-1}) was similar between the dry and wet seasons within each study site (Fig. 7b). However, both LAI and canopy conductance (g_C, mm s^{-1}) were consistently lower during the dry season and in many cases the differences were significant at either $P \leq 0.1$ or $P \leq 0.01$ (Fig. 7c and d).

There was no significant relationship between E and air saturation deficit (D) when using all data from the wet and dry
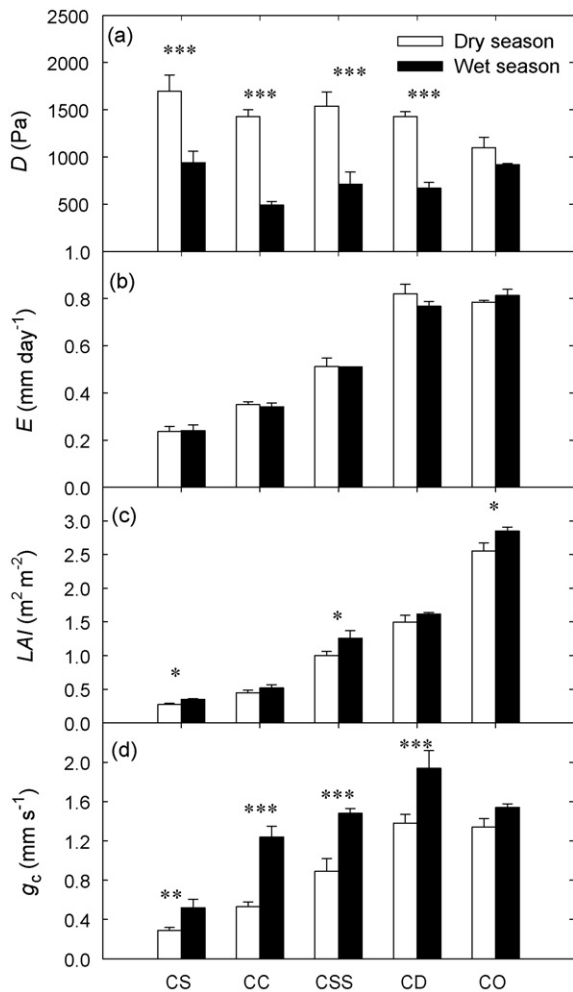

Fig. 7 – (a) Air saturation deficit, D, (b) stand transpiration, E (c) leaf area index, LAI, and (d) canopy conductance, g_C during the dry and wet seasons for five different Cerrado physiognomies. Each bar represents the mean value (±S.E.) for several measurement days (n = 3 to 4) during 3 or 4 months during the dry and wet seasons. Values of g_C represent daily means between 06.00 and 18.00 h. Significant difference between seasons is indicated: *, P < 0.10, **, P < 0.05 and ***, P < 0.01. Letters on the X-axis correspond to the following physiognomies: CO: cerradão, CD: cerrado denso, CSS: cerrado sensu stricto, CC: campo cerrado; CS: campo sujo.
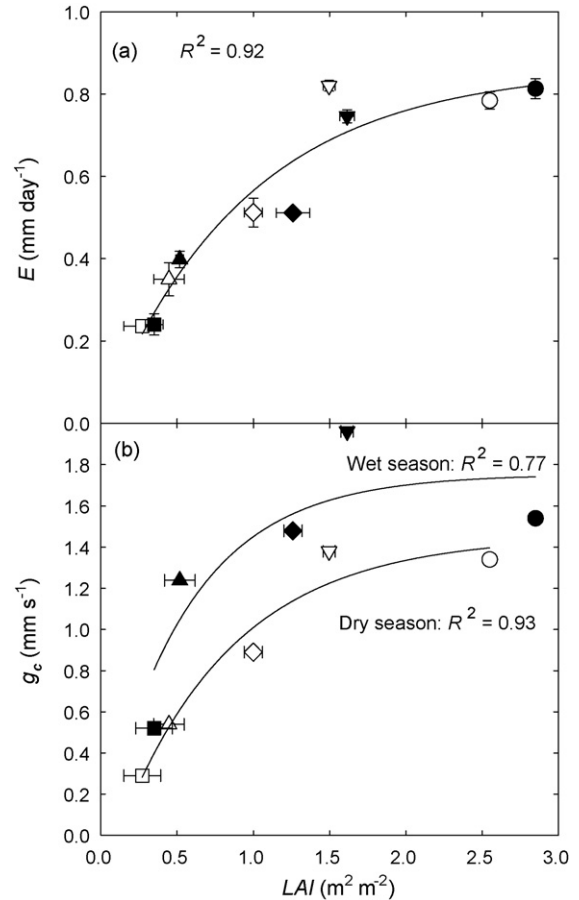

Fig. 8 – (a) Stand transpiration (E) and (b) canopy conductance (g_C,) in relation to leaf area index (LAI) during the dry (open symbols) and wet (closed symbols) seasons for five different Cerrado physiognomies. Each point represents the mean value (±SE) of E or g_C for three to four measurement days during 3–4 months of each season and of LAI during 3 months of each season. Values of g_C represent daily means between 06.00 and 18.00 h. The curves are exponential functions fitted to the data: (a) y = 0.9(1 − exp(−1.1x), P < 0.01; (b) wet season: y = −1.7 + 10(11 − exp(−1.7x), P < 0.05; dry season: y = 1.5(1 − exp(−9.8x), P < 0.005. Symbols as in Fig. 3.

seasons with stand transpiration remaining approximately constant as D varied from about 0.2 to 2.3 kPa (data not shown). Seasonal and site-dependent variation in LAI was a good predictor of both E and g_C (Fig. 8). The dependence of E on LAI was well described by a single asymptotic function (Fig. 8a). However, separate asymptotic functions were necessary to describe the dependence of g_C on LAI during the wet and dry seasons because g_C was consistently higher during the wet season (Fig. 8b). While LAI increased approximately three-fold from campo sujo to cerradao (low to high tree density, respectively), the LAI (m^2 m^{-2})/sapwood area (cm^2 m^{-2}) ratio remained fairly constant along the tree density gradient (results not shown), with exception of the campo sujo that had a significantly lower ratio (P < 0.05). This ratio reflects the relationship between the potential demands of water to

the potential supply of water to the transpiring leaves at a stand level. As expected, dry season LAI/sapwood area were significantly lower ($P < 0.05$) compared to wet season ratios (0.24 versus 0.29 for average dry and wet seasons, respectively) across all physiognomies.

4. Discussion

4.1. Scaling of sap flux to whole-tree and stand levels

Estimating the contribution of trees to total transpiration in savanna ecosystems requires careful assessment of measurements and algorithms used at different scales. Estimates of E based on measurements of J_S are potentially influenced by baseline errors in J_S measurements, systematic spatial variation in J_S within stems and a lag between water uptake and transpiration caused by hydraulic capacitance (Ewers and Oren, 2000; Meinzer et al., 2003). If the sapwood is thick, several sap flow probes installed at different depths and at different positions around the stem may be necessary for accurate estimates of total sap flow per tree (e.g. Meinzer et al., 2004). However, in small trees with relatively thin sapwood, one probe may provide adequate estimates of whole-tree sap flow (e.g. Bucci et al., 2005). Although exchange of water between stem storage compartments and the transpiration stream may affect point measurements of J_S, the effect is transient and not relevant for calculating daily stand-level transpiration. Because most of the dominant species were included in the sap flow measurements, the scaling of sap flow from individual trees to the stand was straightforward (Eq. (1)). Furthermore, the average basal area of all the trees used for sap flow measurements in each site was similar to the average basal area of all trees in each physiognomic type. An alternative scaling method was also used that provided similar results. The method consisted of using all data obtained during both the wet and dry seasons in all five study sites to derive a linear relationship between sap flow (F) and basal area (BA) per tree ($F = 0.04BA + 0.524$; $r^2 = 0.62$, $P < 0.001$). Therefore, basal area was a good predictor of sap flow per tree regardless of species identity. Stand transpiration for each site was then obtained by multiplying the basal area of each tree per site times the predicted sap flow using the linear scaling relationship and then summing all sap flows. These estimates of stand transpiration tended to be slightly lower than those obtained using Eq. (1). For example the cerrado denso weighted average of transpiration was 0.73 mm day^{-1} and the estimates using the scaling equation were 0.81 mm day^{-1}. This scaling relationship suggests that tree size is more important than species identity for Cerrado woody species and it is consistent with results of a previous study in the Cerrado by Meinzer et al. (1999). Other scaling approaches exist depending on the objective and characteristics of the woody vegetation (Hatton et al., 1995; Dawson, 1996; Allen et al., 1999; Granier et al., 2000; Ewers et al., 2001; Phillips et al., 2002).

Recent findings of convergence in functioning among phylogenetically diverse tree species make scaling of transpiration from the tree to stand level more tractable in high species diversity ecosystems. For example Enquist et al. (1998) found that the total daily water use among 37 plant species

scaled with stem diameter in a similar manner, Bucci et al. (2004) found that wood density was a good predictor of total daily transpiration within and between several Cerrado woody species, and Meinzer et al. (2005) reported that total daily water use scaled as a single sigmoid function of stem diameter among 17 angiosperm tree species in three tropical sites. However, there is insufficient information to determine whether the dependence of sapwood area and sap flow on tree size or wood density is essentially universal for all types of trees.

4.2. Environmental and tree density effects on stand transpiration, LAI, and canopy conductance

Maximum canopy conductance was about 1.8 mm s^{-1} (72 mmol m^{-2} s^{-1}) in the cerrado denso and cerradão sites during the rainy season. Canopy conductance was lower (0.3 mm s^{-1} = 12 mmol m^{-2} s^{-1}) in the low tree density physiognomies and during the dry season across all sites. These values were within the range of those reported for Australian savannas during the dry season (Eamus et al., 2001; Hutley et al., 2001). Canopy conductance is determined by several factors, including environmental variables such as solar radiation, soil water availability, and air saturation deficits (D), and vegetation characteristics such as LAI. Typically, g_C initially increases steeply with LAI, then saturates at higher values of LAI. In contrast, g_C declines as D and soil water deficits increase. In the present study, seasonal adjustments in g_C resulted in a lack of seasonality in E across all sites, despite substantially higher mean D during the dry season (Fig. 7). The reduction in LAI during the dry season cannot fully account for the decline in g_C suggesting that stomatal closure was also responsible for this decline.

Mean daily canopy resistance (r_C) increased linearly with mean daily D in all sites (Fig. 3), but the slopes of the r_C versus D relationships decreased with increasing tree density across sites, suggesting site-specific differences in the responsiveness of r_C to changes in bulk atmospheric evaporative demand (Fig. 4). However, these results do not necessarily imply that inherent stomatal responsiveness to D differed among sites because the relevant value of D to which stomata respond is that imposed at the leaf surfaces, not bulk atmospheric D. It is likely that variation in the D perceived by stomata at the leaf surfaces was more attenuated by the decoupling influence of leaf and canopy boundary layers in Cerrado sites with higher woody plant density than in sites with more sparse woody vegetation. In a study on fluxes of carbon, water and energy in an area of campo cerrado, Miranda et al. (1997) found that the decoupling coefficient, Ω (Jarvis and McNaughton, 1986) was 0.17 during the dry season, which suggest that open Cerrado physiognomies are closely coupled to the atmosphere. In contrast, estimates of Ω ranging from 0.3 to 0.9 for tropical forest stands (Jarvis and McNaughton, 1986; Roberts et al., 1990; Meinzer et al., 1997) are consistent with greater decoupling between leaves and the atmosphere in the stands with the highest tree density and LAI.

A global empirical scaling index developed by Baldocchi and Meyers (1998) for predicting LAI of vegetation based on foliar nitrogen concentration (N), annual precipitation (P) and annual potential evapotranspiration (E_{eq}) was adapted for

savannas by Eamus et al. (2001) who substituted tree density for LAI as the dependent variable because of the strong correlation between these two variables in savannas. They found that tree density in Australian savannas spanning a rainfall gradient of almost 1500 mm was well predicted using an equation of the form:

$$\text{tree density} = (N)\frac{P}{E_{eq}}$$

Baldocchi and Meyers (1998) considered the ratio of P/E_{eq} to be a surrogate for water availability. In the Cerrado, however, neither P nor E_{eq} changes appreciably over the short distances of a few km despite large changes in tree density of the present study. Instead, it is possible that pronounced variations in tree density over short distances in the Cerrado may result from differences in water availability associated with differential access to the water table by deep roots. Although systematic studies of water table depth and its seasonal variation have not been reported for Cerrado vegetation along tree density gradients, existing information for this study area indicates that water tables may occur at about 10 m from the soil surface in denser physiognomies and at a shorter distance in sites with low tree density (Villalobos unpublished information). If these observations are confirmed by further studies, trees in low tree density physiognomies should have access to more abundant and stable water sources than trees in high density stands contrary to predictions of the model of Eamus et al. (2001). We suggest that water availability may not be an important determinant of tree density over short distances in the Cerrado and that variations in nutrient availability are likely to be a major determinant of spatial variation in tree abundance. In a previous study, we found that Cerrado woody species responded to long-term N fertilization by increasing total leaf area, basal area and water use per tree (Bucci et al., 2006). Thus, we hypothesize that variations in tree density along topographic gradients in the Cerrado are partially determined by variations in soil nutrient availability. Nutrient limitation in Cerrado ecosystems (Haridasan, 2000, 2001) may also explain why E saturated at low LAI (~1.5) compared to E versus LAI relationships observed in others ecosystems (e.g. Al-Kaisi et al., 1989; Delzon and Loustau, 2005). Even at the highest LAI's observed in our study sites, self-shading should still be low, making increasing light attenuation an unlikely cause of the asymptotic relationship between E and LAI.

4.3. Patterns of water utilization and tree density

During the peak of the dry season the Ψ_{soil} at 0.20 m depth became increasingly negative with decreasing woody plant density (Fig. 5a). This somewhat unexpected trend was probably attributable to greater abundance of shallow-rooted herbaceous plants and higher soil water evaporation in sites with lower woody plant density. Wet-season grass LAI across these study sites declined with increasing tree density, ranging from 1.29 in most open sites to 0.35 in the densest sites (Hoffmann et al., 2005). Herbaceous Cerrado species rapidly exhaust available water in the upper portion of the soil profile and undergo rapid declines in LAI throughout the dry season (Hoffmann et al., 2005). Access to soil water by trees

appears to be little influenced by herbaceous plants due to decreases in herbaceous layer LAI during the dry season, in low tree density physiognomies, and the low LAI of the herbaceous layer in the physiognomies with high tree density. Although Cerrado woody species tend to access deeper soil water sources than herbaceous species, there are differences in the patterns of water uptake between deciduous and evergreen species and among evergreen species as well (Jackson et al., 1999; Scholz, 2006), which have profound implications for regulation of tree water balance, as well as processes related to hydrological cycles in Cerrado ecosystems. Deciduous and brevideciduous Cerrado tree species that hydraulically lift water tend to have conspicuously dimorphic root systems with an extensive network of shallow roots and one or more major descending roots (Scholz et al., 2002; Moreira et al., 2003; Scholz, 2006). Soil water storage between 0.10 and 2.50 m decreased abruptly at the beginning of the dry season in the three sites with the highest tree density, and gradually in the campo sujo and campo cerrado sites (Fig. 6). Late in the dry season, water storage in the upper 2.50 m of soil decreased by about 200 mm in the cerradao site and only 80 mm in the campo sujo, indicating greater utilization of deeper soil water resources with increasing abundance of woody plants. Similar observations were reported by Quesada et al. (2004) in campo sujo and cerrado sensu stricto sites subjected to different fire frequency. Differences in vertical partitioning of soil water resources among woody and herbaceous species contributed to the inverse relationship between water stored in the upper 2.50 m of soil and Ψ_{soil} at 0.20 m (Fig. 5a and b). In sites dominated by herbaceous species water at depth remained untapped while physiologically available water in the upper soil was depleted.

4.4. Conclusions

Overall, the results of this study show that there was little seasonality of tree transpiration in each site along a gradient of tree density, despite strong seasonality in D and precipitation. Seasonal stability of E, from plant to ecosystem, could not be explained by individual constraining variables, but was consistent with the influence of multiple regulatory effects of D and soil water potential on leaf area dynamics and g_C. For both dry and wet season data combined, E and g_C increased asymptotically with increasing LAI across al physiognomic types. Consequently spatial variations in stand-level tree transpiration were closely related to variations in site-specific tree LAI. Scaling stem sap flow to whole-tree and stand-level tree transpiration in different savanna physiognomic types during wet and dry seasons was a powerful approach for understanding regulatory mechanisms of water cycles in savanna ecosystems.

REFERENCES

Allen, S.J., Hall, R.L., Rosier, P.T.W., 1999. Transpiration by two poplar varieties grown as coppice for biomass production. Tree Physiol. 19, 493–501.

Al-Kaisi, M., Brun, L.J., Enz, J.W., 1989. Transpiration and evapotranspiration from maize as related to leaf area index. Agric. For. Meteorol. 48, 111–116.

Asner, G.P., Wessman, C.A., Archer, S., 1998. Scale dependence of absorption of photosynthetically active radiation in terrestrial ecosystems. Ecol. Appl. 8, 1003–1021.

Baldocchi, D., Meyers, T., 1998. On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapour and trace gas fluxes over vegetation: a perspective. Agric. For. Meteorol. 90, 1–25.

Brown, R.W., Bartos, D.J., 1982. A calibration model for screen-caged peltier thermocouple psychrometers. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. Research paper INT-293.

Bucci, S.J., Goldstein, G., Meinzer, F.C., Scholz, F.G., Franco, A.C., Bustamante, M., 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiol. 24, 891–899.

Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Campanello, P., Scholz, F.G., 2005. Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plants in Neotropical savanna trees. Trees 19, 296–304.

Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., Franco, A.C., Campanello, P.I., Villalobos-Vega, R., Bustamante, M., Miralles-Wilhelm, 2006. Nutrient availability constrains the hydraulic architecture and water relations of savanna trees. Plant Cell Environ. 29, 2153–2167.

Clearwater, M.J., Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., 1999. Potential errors in measurement of no uniform sap flow using heat dissipation probes. Tree Physiol. 19, 681–687.

Dawson, T.E., 1996. Determining water use by trees and forest from isotopic, energy balance and transpiration analysis: the roles of tree size and hydraulic lift. Tree Physiol. 16, 263–272.

Delzon, S., Loustau, D., 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. Agric. For. Meteorol. 129, 105–119.

Do, F., Rocheteau, A., 2002. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 1. Field observations and possible remedies. Tree Physiol. 22, 641–648.

Eamus, D., Hutley, L.B., O'Grady, A.P., 2001. Daily and seasonal patterns of carbon and water fluxes above and north Australia savanna. Tree Physiol. 21, 977–988.

Enquist, B.J., Brown, J.H., West, G.B., 1998. Allometric scaling of plants energetic and population density. Nature 395, 164–165.

Ewers, B.E., Oren, R., 2000. Analysis of assumptions and errors in the calculations of stomatal conductance from sap flux measurements. Tree Physiol. 20, 579–589.

Ewers, B.E., Oren, R., Jonshen, K.H., Landsberg, J.J., 2001. Estimating maximum stomatal conductance for use in models. Can. J. For. Res. 31, 198–207.

Felfili, J.M., Haridasan, M., Cunha de Mendoca, R., Filgueiras, T., Silva, M.C., Rezende, A.V., 1994. Projeto biogeografia do bioma cerrado: vegetacão e solos. Cadernos de Geociencias, Rio de Janeiro October/December, 75–166.

Ford, C.R., McGuire, M.A., Mitchell, R.J., Teskey, R.O., 2004. Assessing variation in the radial profile of the sap flow

density in Pinus species and its effects on daily water use. Tree Physiol. 24, 241–249.

Granier, A., 1985. Une nouvelle méthode pour la mesure du flux de séve brute dans le tronc des arbres. Ann. For. Sci. 42, 193–200.

Granier, A., 1987. Evaluation of transpiration in a Douglas fir stand by mean of sap flow measurement. Tree Physiol. 3, 309–320.

Granier, A., Loustau, D., 1994. Measuring and modeling the transpiration of a maritime pine canopy from sapflow data. Agric. For. Meteorol. 71, 61–81.

Granier, A., Biron, P., Breda, N., Pontailler, J.-Y., Saugier, B., 1996. Transpiration of trees and forest stands: short and long term monitoring using sap flow methods. Global Change Biol. 2, 265–274.

Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. Agric. For. Meteorol. 100, 291–308.

Haridasan, M., 2000. Nutrição mineral de plantas nativas do cerrado. Braz. J. Plant Physiol. 12, 54–64.

Haridasan, M., 2001. Nutrient cycling as a function of landscape and biotic characteristics in the cerrado of central Brazil. In: McClain, M.E., Victoria, R.L., Richey, J.E. (Eds.), Biogeochemistry of the Amazon basin and its role in a changing world. Oxford University Press, New York, p. 68-83, 357p.

Hatton, T.J., Moore, S.T., Reece, P.H., 1995. Estimating stand transpiration in a Eucalyptus papulnea woodland with the heat pulse method: measurements errors and sampling strategies. Tree Physiol. 15, 219–227.

Heringer, E.P., Barroso, G.M., Rizzo, J.A., Rizzine, C.T., 1977. A flora do Cerrado. In: Ferri, M.G. (Ed.), IV Simposio sobre o Cerrado. Editora Universidade de Sao Paulo, Sao Paulo, Brazil, pp. 211–232.

Hoffmann, W.A., Silva, E., Machado, G., Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., 2005. Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. Oecologia 145, 307–316.

Hutley, L.B., O'Grady, A.P., Eamus, D., 2001. Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia. Oecologia 126, 434–443.

Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A.C., Rundel, P.W., Caldas, L., Igler, E., Causin, F., 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. Tree Physiol. 19, 717–724.

Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration. Eds. A. Mcfadyen and D.E. Ford. Adv. Ecol. Res. 15, 1–49.

Kostner, B., Granier, A., Cemark, J., 1998. Sap flow methods in forest stands: methods and uncertainties. Ann. For. Sci. 55, 13–27.

Martin, T.A., Brown, K.J., Cermak, J., Ceulemans, R., Kucera, J., Meinzer, F.C., Rombold, J.S., Sprugel, D.G., Hinckley, T.M., 1997. Crown conductance and tree and stand transpiration in a second-growth Abies amabilis forest. Can. J. For. Res. 27 (6), 797–808.

McCulloh, K.A., Winter, K., Meinzer, F.C., Garcia, M., Aranda, J., Lachenbruch, B., 2007. A comparison of daily water use estimates derived from constant-heat sap-flow probe values and gravimetric measurements in pot-grown saplings. Tree Physiol. 27, 1355–1360.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavalier, J., Jackson, P., 1997. Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. Plant Cell Environ. 20, 1242–1252.

Meinzer, F.C., Goldstein, G., Franco, A.C., Bustamante, M., Igler, E., Jackson, P., Caldas, L., Rundel, P.W., 1999. Atmospheric

and hydraulic limitations on transpiration in Brazilian cerrado woody species. Funct. Ecol. 13, 273–282.

Meinzer, F.C., James, S.A., Goldstein, G., Woodruff, D., 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant Cell Environ. 26, 1147–1155.

Meinzer, F.C., James, S.A., Goldstein, G., 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiol. 24, 901–909.

Meinzer, F.C., Bond, B.J., Warren, J.M., Woodruff, D.R., 2005. Does water transport scale universally with tree size? Funct. Ecol. 19, 558–565.

Miranda, A.C., Miranda, H.S., Lloyd, J., Grace, J., Francey, R.J., Mcintyre, J.A., Meir, P., Riggan, P., Lockwood, R., Brass, J., 1997. Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. Plant Cell Environ. 20, 315–328.

Monteith, J.L., Unsworth, M.H., 1990. Principals of Environmental Physics, 2nd ed. Edward Arnold, London.

Moreira, M.Z., Scholz, F.G., Bucci, S.J., Sternberg, L.S., Goldstein, G., Meinzer, F.C., Franco, A.C., 2003. Hydraulic lift in a Neotropical savanna. Funct. Ecol. 17, 573–581.

Oren, R., Zimmermann, M., Terborgh, J., 1996. Transpiration in upper Amazonia floodplain and upland forest in response to drought breaking rains. Ecology 77, 968–973.

Oren, R., Phillips, N., Katul, G., Ewer, B.E., Pataki, D.E., 1998. Scaling xylem sap flow and soil water balance and calculating variance. A method for partitioning water flux in forests. Ann. For. Sci. 55, 191–216.

Pataki, D.E., Oren, R., Smith, W.K., 2000. Transpiration of co-occurring species in a western subalpine forest during seasonally developing drought. Ecology 81, 2557–2566.

Paltineanu, I.C., Starr, J.L., 1997. Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. Soil Sci. Soc. Am. J. 61, 1576–1585.

Phillips, N., Oren, R., Zimmermann, R., 1996. Radial patterns of xylem sap flow in non-diffuse and ring porous tree species. Plant Cell Environ. 19, 983–990.

Phillips, N., Oren, R., 1998. A comparison of daily representations of canopy conductance based in two conditional time-averaging methods and the dependence of daily conductance on environmental factors. Ann. Sci. For. 55, 217–235.

Phillips, N., Bond, B.J., McDowell, N.G., Ryan, M.G., 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiol. 22, 205–211.

Quesada, C.A., Miranda, A.C., Hodnett, M.G., Santos, A.J.B., Miranda, H.S., Breyer, L.M., 2004. Seasonal and depth variations of soil moisture in a burned open savanna (*campo sujo*) in Central Brazil. Ecol. Appl. 14 (4), S33–S41.

Roberts, J., Cabral, O.M.R., De Aguiar, L.F., 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. J. Appl. Ecol. 27, 336–353.

Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., 2002. Hydraulic redistribution of soil water by Neotropical savanna trees. Tree Physiol. 22, 603–612.

Scholz, F.G., 2006. Biofísica del transporte de agua en el sistema suelo-planta: redistribución, resistencias y capacitancias hidráulicas. PhD. Thesis. Universidad de Buenos Aires, Argentina, p. 79.

Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Miralles-Wilhelm, F., 2007. Biophysical properties and functional significance of stem water storage tissues in neo-tropical savanna trees. Plant Cell Environ. 30, 236–248.

Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Miralles-Wilhelm, F., in press. Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. Tree Physiol.