



Water relations and hydraulic architecture in Cerrado trees: adjustments to seasonal changes in water availability and evaporative demand

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We determined adjustments in physiology and morphology that allow Neotropicsavanna trees from central **Brazil** (Cerrado) to avoid water deficits and to maintain a nearly constant internal water balance despite seasonal changes in precipitation and air saturation deficit (D). Precipitation in the study area is highly seasonal with about five nearly rainless months during which D is two fold higher compared to wet season values. As a consequence of the seasonal fluctuations in rainfall and D, soil water potential changes substantially in the upper 100 cm of soil, but remains nearly constant below 2 m depth. Hydraulic architecture and water relations traits of Cerrado trees adjusted during the dry season to prevent increasing water deficits and insure homeostasis in minimum leaf water potential Ψ_L and in total daily water loss per plant (isohydry). The isohydric behavior of Cerrado trees was the result of a decrease in total leaf surface area per tree, a strong stomatal control of evaporative losses, an increase in leaf-specific hydraulic conductivity and leaf hydraulic conductance and an increase in the amount of water withdrawn from internal stem storage, during the dry season. Water transport efficiency increased in the same proportion in leaves and terminal stems during the dry season. All of these seasonal adjustments were important for maintaining Ψ_L above critical thresholds, which reduces the rate of embolism formation in stems and help to avoid turgor loss in leaf tissues still during the dry season. These adjustments allow the stems of most Cerrado woody species to operate far from the point of catastrophic dysfunction for cavitation, while leaves operate close to it and experience embolism on a daily basis, especially during the dry season.

Key words: isohydric behavior, hydraulic conductivity, soil water potential and water content, savanna, stomatal conductance, transpiration

Relações hídricas e arquitetura hidráulica em árvores do cerrado: adequação às variações sazonais de disponibilidade hídrica e de demanda evaporativa: O objetivo deste estudo foi determinar os ajustamentos na morfologia e fisiologia que permitem árvores das savanas neotropicais do Brasil Central (Cerrado) de evitar déficits hídricos e de manter um balanço hídrico interno praticamente constante apesar das variações sazonais da precipitação e no deficit de saturação do ar (Δ). A precipitação na área de estudo é fortemente sazonal, com cerca de cinco meses praticamente sem chuva durante os quais Δ é duas vezes maior aos valores medidos na época chuvosa. Como consequência da flutuação sazonal das chuvas e de Δ , o potencial hídrico do solo muda substancialmente, nos primeiros 100 cm do solo, mas permanece quase

constante abaixo de 2 m de profundidade. A arquitetura **hidráulica** e os **parâmetros** relacionados a **relações** hídricas das **árvores** do Cerrado se ajustaram durante a **estação** seca para evitar o **déficit** hídrico crescente e assegurar a homeostase nos valores mínimos de potencial hídrico foliar Ψ_L . A perda total **diária** de **água** pela planta (iso-hídria). O comportamento iso-hídrico das **árvores** do Cerrado foi o resultado de **uma diminuição** da superfície foliar total **por** árvore, um forte controle estomático das perdas por **evaporação**, um aumento na condutividade **hidráulica específica** da folha e **na condutância hidráulica** foliar e um aumento da quantidade de **águas retirada** dos reservatórios internos do caule, durante a **estação** seca. A **eficiência** no transporte de **água** aumentou, nas mesmas **proporções**, nas folhas e nos ramos terminais durante a **estação** seca. Todos estes ajustamentos sazonais foram importantes para a **manutenção** de Ψ_L acima de limiares críticos, com isto contribuindo para uma **redução** na **formação** de embolismos nos ramos e ajudando a evitar a perda de turgor em tecidos foliares durante a **época seca**. Esses ajustes permitem que os ramos das **espécies** lenhosas do Cerrado operem bem distanciados do ponto de **disfunção** catastrófica para **acavitação**, enquanto as folhas operam próximas e sofrem embolismos em lima base diária, especialmente durante a **estação** seca.

Palavras-chave: comportamento iso-hídrico, condutividade hidráulica, potencial hídrico do solo e conteúdo de **água**, savana, **condutância** estomática, **transpiração**

INTRODUCTION

Trees growing in tropical environments characterized by distinct wet and dry seasons have to seasonally adjust their morpho-physiological traits to cope successfully **with** changes in **soil water availability**. Intuitively the most obvious responses of a plant to cope with limited water **availability** in a strong seasonal environment would be a reduction in transpiration by stomatal limitation and/or dropping the leaves to further decrease evaporative water loss during the dry season. Many tree species growing in tropical **dry** forests are deciduous, dropping their leaves at the beginning of the dry season and producing a new crop of leaves at the beginning of the wet season (Borchert, 1994; Rivera et al., 2002). Their seasonal growth rates are well coupled to the seasonal changes in the availability of the main limiting resource: water. In contrast, physiological activity and growth rates of savanna trees are uncoupled from seasonal changes in precipitation (Gouveia, 1998; Meinzer et al., 1999; Prado et al., 2004; Simioni et al., 2004; Damascos et al., 2005; Bucci et al., 2005; Franco et al., 2005; Hoffmann et al., 2005). even though the seasonal pattern of precipitation is similar to that of dry forests. Indeed, seasonally deciduous or semideciduous forests occur throughout the savanna region in Central Brazil on rich Ca and Mg soils (Ratter et al., 1978).

The climate of savanna ecosystems of Central Brazil (**Cerrado**) is characterized by five months with very few rainfall events and a long period with high precipitations. Evaporative demand is substantially higher during the

dry season (May to September) because of lower ambient relative humidity. The combination of higher evaporative demand and low precipitation during the **dry** season makes the Cerrado a potentially stressful environment for vascular plants. Despite stressful conditions during the rainless season, many tree species maintain an active crop of leaves during this period and new leaves are produced before the beginning of the wet season (Franco et al., 2005; Lenza and Klink, 2006). Stem growth rates increase after the first large rainfall pulses of the wet season and high growth rates are maintained **until** two to three months before the end of the wet season in early March (Saraceno, 2006). It is likely that photo-assimilates, at this point in time, are channeled to enhance root growth, instead of stem growth, to insure water uptake during the dry season. The production of new leaves by savanna trees during the most unfavorable period for growth may be an adaptive response to the low nutrient availability in the soil (Sarmiento et al., 1985). The presence of completely expanded leaves before the first rainfall events can help to reduce nutrient leaching from leaves because their cuticle would be fully developed, making them less leachable compared to expanding leaves. Minimizing nutrient losses and at the same time decreasing leaf losses to herbivores, which are less active at the end of the dry season (Marquis et al., 2002), is advantageous in terms of nutrient and carbon balance. Nevertheless, maintaining leaves as **well** as producing new leaves **during** the dry season incurs a carbon cost for savanna trees. They have to cope with

the higher cost of maintaining **long** and **deep roots** to tap water from abundant and more **stable** water sources available at depth (Scholz et al., 2008a). **Even** though most Cerrado trees have more than 50% of their biomass belowground (Sarmiento, 1983; Castro and Kauffman, 1998), some Cerrado **woody** species have relatively shallow root **systems** (Scholz et al., 2008a).

To avoid losing leaves during the unfavorable growth period, species from other seasonal **ecosystems** undergo osmotic adjustment in their **photosynthetic** and other metabolically active tissues to avoid losing cell turgor when water is depleted in the **soil** and plant water potential becomes more negative. Other **changes** in leaf-water relations **characteristics** may include a **decrease** in the modulus of elasticity (Turner and Jones, 1980). However, if woody Cerrado **species** are isohydric (Franco, 1998; Meinzer et al., 1999; Prado et al., 2004; Bucci et al., 2005), then osmotic adjustment or any other change in pressure volume relationships in leaves during the dry season may **not** be needed. **Different** types of physiological and morphological adjustments that allow the **trees** to maintain leaf water potentials (Ψ_L) **above** the turgor **loss** point **during** the dry season are possible. The first objective of this study **was** to assess if dominant Cerrado woody species are isohydric, meaning that they maintain similar minimum Ψ_L throughout the year (Tardieu and Simonneau, 1998). The term isohydry is used interchangeably with homeostasis in minimum Ψ_L in this study. The second objective was to discuss the current knowledge and new data concerning physiological and morphological adjustments which favor the water balance of Cerrado woody **species** during the dry season. The third objective was to assess the **degree** of coordination between stem and leaf hydraulics to help identify additional mechanisms governing the regulation of internal water balance of savanna trees.

MATERIAL AND METHODS

Study site and plant material: The study was conducted in savanna sites with intermediate **tree** density (cerrado sensu stricto) 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). Annual precipitation in the reserve ranges from 880 to 2150 mm depending on the year with a

mean of approximately 1500 mm (www.recor.org.br). There is a pronounced dry season from May through September with the months of June, July and **August** being nearly rainless. Mean monthly temperature ranges from 19 to 23 °C with diurnal temperature variations of 20 °C being common during the dry season. The soils are **deep** oxisols containing about 70% clay. The development of micro aggregate structures (e.g. cementation by iron oxides) allows Cerrado soils to be generally porous and well drained despite their high clay content (Furley and Ratter, 1988).

An extensive data set collected over 10 years (1996 to 2006) from 12 dominant woody **species** ranging from evergreen to brevid deciduous and deciduous (Meinzer et al., 1999; Bucci et al., 2004a,b; Bucci et al., 2005; Bucci et al., 2006; Scholz et al., 2006; Scholz et al., 2007; Bucci et al., 2008; Goldstein et al., 2008; Hao et al., 2008; Scholz et al., 2008a,b) was used in this study in addition to previously unpublished data. The species studied, their family, leaf phenology and measured morphological and physiological variables in each species are listed in Table 1.

Soil water potential and volumetric water content: Soil water potential was measured using soil psychrometers (PST-55, Wescor, Logan, UT) which were deployed at 0.20, 0.30, 0.60 and 1.00 m below the soil surface. The psychrometers were connected to a data logger (CR-7, Campbell Scientific, Logan, Utah, USA). Soil volumetric water content **was** measured with highly sensitive probes containing eight annular capacitance sensors (Sentek PTY LTD, Adelaide, Australia) positioned at several depths down to 250 cm. Technical details for both methods are described in Bucci et al. (2008).

Leaf area index: Leaf area index of woody **species** was estimated with a LAI 2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska, USA) during wet (October, February and April) and dry (May, June and August) seasons as described previously (Hoffmann et al., 2005; Bucci et al., 2008).

Sapwood and leaf water potential, and turgor loss point: Sapwood water potential (Ψ_{-w}) was **measured** in one representative tree per species during the dry season with in situ stem psychrometers (Plant Water Statlits Instruments, Guelph, Ontario, Canada) and recorded with a datalogger (CR-7, Campbell Scientific, Logan, UT, USA) at 10-min intervals as described in Scholz et al. (2007).

Table 1. **Species studied** and family, leaf phenology and measured variables in each **species**.

Species	Phenology	Variables
<i>Byrsonima crassa</i> Nied. (Malphigiaceae)	Brevidciduous	$K_{\text{Leaf}}, K_L, Lp, A_L:A_S, E, \Psi_L, \Psi_{\text{sw}}, P_{\text{stem}}^{50}, P_{\text{leaf}}^{50}, g_s, \pi^0$
<i>Blepharocalyx salicifolius</i> (R.B.K.) Berg (Myrtaceae)	Brevidciduous	$K_{\text{Leaf}}, K_L, Lp, A_L:A_S, E, \Psi_L, \Psi_{\text{sw}}, P_{\text{stem}}^{50}, P_{\text{leaf}}^{50}, g_s, \pi^0, \text{ws}$
<i>Caryocar brasiliense</i> Camb. (Caryocaraceae)	Brevidciduous	$K_L, A_L:A_S, E, \Psi_L, g_s, \pi^0, \text{ws}$
<i>Elythroxyllum suberosum</i> St. Hi! (Erythroxylaceae)	Brevidciduous	$K_L, A_L:A_S, E, \Psi_L, g_s$
<i>Kielmeyera coriacea</i> (Spr.) Mart (Clusiaceae)	Deciduous	$K_{\text{Leaf}}, K_L, Lp, A_L:A_S, E, \Psi_L, \Psi_{\text{sw}}, P_{\text{stem}}^{50}, P_{\text{leaf}}^{50}, g_s, \pi^0, \text{ws}$
<i>Ouratea hexasperma</i> Baill (Ochnaceae)	Evergreen	$K_L, A_L:A_S, E, \Psi_L, g_s, \pi^0$
<i>Qualea parviflora</i> Mart. (Vochysiaceae)	Deciduous	$K_{\text{Leaf}}, K_L, Lp, K_L, A_L:A_S, E, \Psi_L, \Psi_{\text{sw}}, P_{\text{stem}}^{50}, P_{\text{leaf}}^{50}, g_s, \pi^0$
<i>Roupala montana</i> Aubl. (Proteaceae)	Evergreen	
<i>Schefflera macrocarpa</i> Seem D.C. Frodin (Araliaceae)	Evergreen	$K_L, A_L:A_S, E, \Psi_L, g_s, \pi^0, \text{ws}$
<i>Sclerolobium paniculatum</i> Vog. (Leguminosae)	Evergreen	$\Psi_L, \Psi_{\text{sw}}, g_s, \pi^0, \text{ws}$
<i>Styrax ferrugineus</i> Nees & Mart. (Styracaceae)	Evergreen	$K_L, A_L:A_S, E, \Psi_L, \Psi_{\text{sw}}, P_{\text{stem}}^{50}, P_{\text{leaf}}^{50}, g_s, \pi^0$
<i>Vochysia thyrsoidea</i> Mart. (Vochysiaceae)	Evergreen	$K_L, A_L:A_S, E, \Psi_L, g_s, \pi^0, \text{ws}$

Minimum leaf water potential (Ψ) was measured with a pressure chamber (PMS Instruments, Corvallis OR, USA) in three exposed leaves on each of three to five individuals per species during the dry season (August–September) and wet season (February–March). The bulk leaf turgor loss point (π^0) was determined from pressure–volume relationships (Tyree and Hammel, 1972) for three, fully developed exposed leaves from three individuals per species during the dry and wet seasons.

Root and leaf hydraulic properties and stomatal conductance: Total hydraulic conductivity (Lp) was measured in roots of *B. crassa*, *B. salicifolius*, *K. coriacea* and *Q. parviflora* collected between 0530 and 0700 h in January (wet season) and August (dry season) as described in Scholz *et al.*, (2008a). The Lp ($\text{m s}^{-1} \text{MPa}^{-1}$) was calculated as $Lp = (\Delta Q_v / \Delta P) (1/A)$ where Q_v ($\text{m}^3 \text{s}^{-1}$) is volumetric flow rate, P (MPa) is the pressure applied, and A (m^2) is the lateral surface area of the root segment (Nobel, Schulte and North, 1990).

Leaf-specific hydraulic conductivity (K_L ; $\text{kg m}^{-1} \text{s}^{-1}$

MPa^{-1}) was measured in three branches excised before dawn from three to five individuals per species during dry and wet seasons according to Bucci *et al.*, (2004a) and Bucci *et al.*, (2006). Branches were immediately re-cut under water and attached to a hydraulic conductivity apparatus (Tyree and Sperry, 1989). Leaf-specific conductivity was calculated as the mass flow rate divided by the pressure gradient across the branch segment and normalized by the total leaf area distal to the stem. Stem vulnerability curves, to estimate the pressure at 50 percent of loss conductivity (P_{stem}^{50}), were determined by measuring percentage loss of hydraulic conductivity due to embolism over a range of water potential reached during dehydration by the bench drying method (Sperry *et al.*, 1988). Details about stem vulnerability curves are described in Bucci *et al.*, (2006) and Hao *et al.*, (2008).

Leaf hydraulic vulnerability curves were determined measuring leaf hydraulic conductance (K_{leaf}) following the partial rehydration method described by Brodribb and Holbrook, (2003). Three leaves of five different trees per species were used to measure K_{Leaf} and to estimate the

pressure at 50 percent of loss conductivity (P_{leaf}^{50}). Capacitance values both before and after turgor loss point (π^0) were calculated from leaf pressure-volume relations as described in Hao et al., (2008).

A steady state porometer (model LI-1600, LI-COR Inc., Lincoln, Nebraska, USA) was used to measure stomatal conductance (g_s) of three to seven leaves on the same trees used to measure Ψ_L every 2 to 3 h during one day of dry and wet season and the maximum values as taken for this study. New, fully expanded leaves from sun-exposed areas of the crown were used for measurements.

Transpiration and stem water storage: The heat dissipation method (Granier, 1985, 1987) was used to measure the mass flow of water in ten out of the 12 species (three to five individuals per species) during two to five consecutive days at the end of the dry season (August and September) and at the peak of the wet season (January and February). Transpiration per unit leaf area (E) was obtained by dividing the mass flow of sap measured near the base of the main stem of each tree by the total leaf area per plant according to Meinzer et al., (1999) and Bucci et al., (2005). Total leaf area per plant was obtained by multiplying the number of leaves per plant by the average projected area per leaf, determined from a sub-sample of 10-50 leaves per plant.

To determine daily utilization of stored water for transpiration, sap flow was measured simultaneously in terminal branches and near the base of the main stem in six of study species as described in Scholz et al., (2008b). Stem water storage (ws) calculations were based on the method described by Goldstein et al., (1998).

RESULTS

Precipitation in the study area is highly seasonal with about five nearly rainless months (May through September, Figure 1). Mean daily air saturation deficit (O) is twice as great toward the end of the dry season compared to wet season values. As a consequence of the seasonal fluctuations in precipitation and O , soil water potential fluctuated substantially in the upper 100 cm of soil. Average soil water potential, between 20 and 100 cm depth, ranged from 0 MPa in the rainy season to about -2.0 MPa near the end of the dry season (Figure 2a). Soil water storage (the total amount of water in the upper 250 cm of the soil profile excluding the first 10 cm) also

changed seasonally. It decreased from about 400 mm in the wet season to about 230 mm at the peak of the dry season (Figure 2b). This would imply that the vegetation had used about 170 mm of water up to the peak of the dry season if one assumes that the period was rainless, and that there was neither lateral flow nor deep percolation. Tree and shrub leaf area index responded to changes in soil water availability decreasing from $1.4 \text{ m}^2 \text{ m}^{-2}$ in the wet season to about $1 \text{ m}^2 \text{ m}^{-2}$ at the peak of the dry season.

Several scaling relationships between leaf functional traits or between leaf traits and branch architectural traits across species were identified. In some cases only one mathematical function was enough to describe scaling relationships for both wet and dry season data, and in other cases two functions were used to describe dry and wet season relationships. Observed minimum Ψ_L increased linearly with increasing π^0 across species (Figure 3). Minimum Ψ_L and π^0 did not differ between seasons and consequently only one functional relationship was fitted to all data. Leaves of all species were able to maintain positive turgor pressure still during the dry season, with the exception of *O. hexasperma* that reached the turgor loss point during the wet season. The observed minimum Ψ_L and π^0 relationship slope (0.90) did

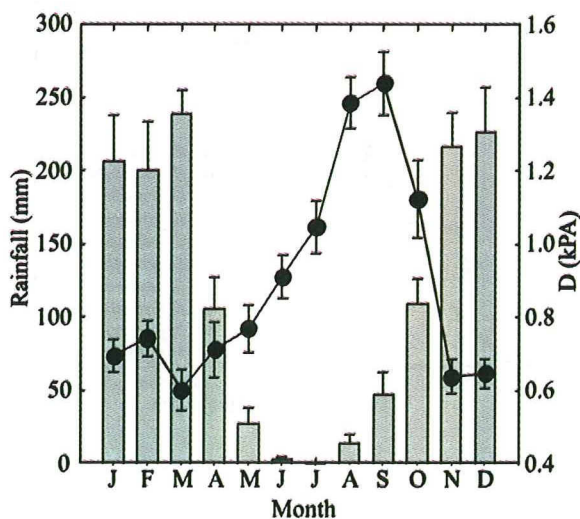


Figure 1. Ten-year monthly average (from 1995 to 2005) precipitation, and air saturation deficits (O), at the IBGE research station near Brasilia, Brazil. Bars are total monthly precipitation and the continuous line is O . Error bars are standard errors. Source: www.recor.org.br,

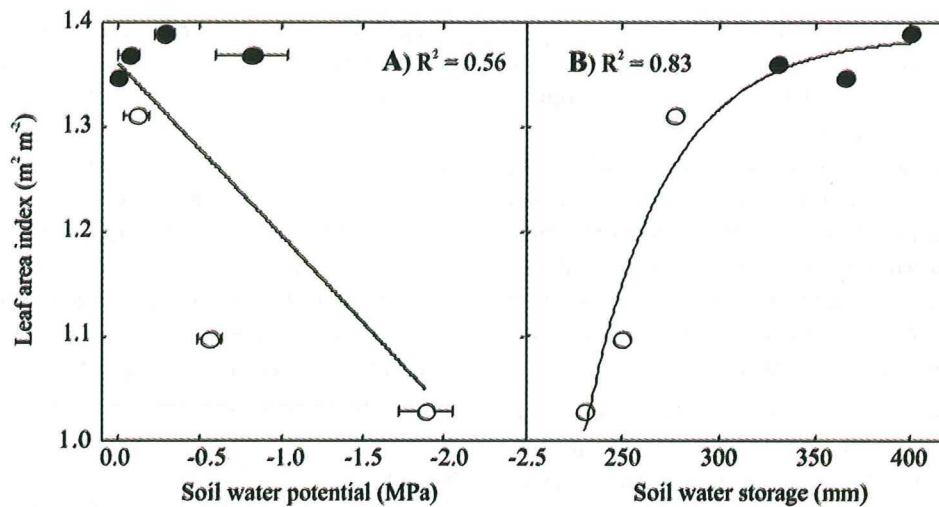


Figure 2. Leaf area index as a function of average soil water potential between 20 and 100 cm depth (a) and soil water storage between 10 and 250 cm depth (b) in a Cerrado site with intermediate tree density. Data points are leaf area index and soil water storage or soil water potential measured during the course of one year, encompassing wet (February and April) and dry (May, June and August) season periods. The line in (a) is the linear regression fitted to the data ($y = -4.83 + 3.37x$; $P = 0.05$). The line in (b) is an exponential rise to a maximum fitted to the data ($y = 1.75 * (1 - \exp(-0.004x))$; $P < 0.05$). Open symbols: dry season and closed symbols: wet season.

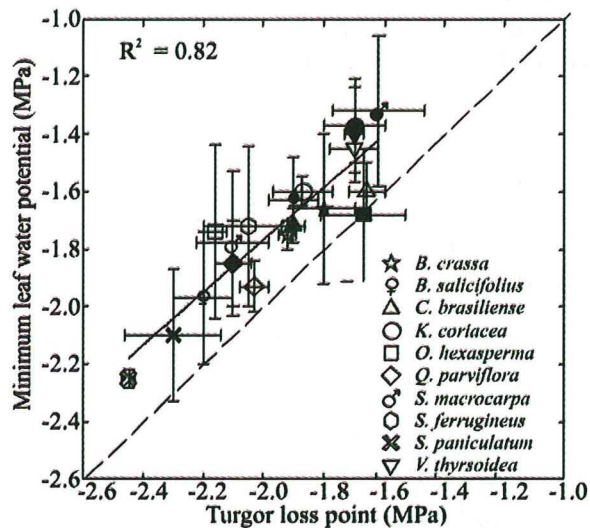


Figure 3. Minimum leaf water potential (Ψ_L) as a function of the osmotic potential at the turgor loss point (π^0) obtained during the wet season (filled symbols) and the dry season (open symbols) for ten dominant woody species. The continuous line is a linear regression fitted to both wet and dry seasons data ($y = -0.40 + 0.90x$; $P < 0.001$). Dashed line is the 1:1 relationship between Ψ_L and π^0 . Values are means $\pm$ SE of three to five individuals per species.

not differ significantly from 1 indicating that turgor pressure at minimum Ψ_L was more or less constant across species and seasons. Midday Ψ_L increased with increasing maximum stomatal conductance measured at mid-morning; however linear relationships were fitted separately for wet and dry season data (Figure 4). Even though there were not species-specific differences in midday Ψ_L between seasons, stomatal conductance tended to be several fold lower in the dry season compared to the wet season ($P < 0.001$).

Observed minimum Ψ_L was less negative with increasing water used from internal stem water storage across species (Figure 5). Utilization of stored water was about 10 % greater during the dry season compared to the wet season. Although the slopes of the relationships between minimum Ψ_L and stored water utilization were similar, the y-intercepts were significantly different ($P < 0.005$).

Transpiration per unit leaf surface area increased with increasing K_L (Figure 6). Transpiration and K_L were higher during the dry season compared to the wet season values for each species studied. A single functional relationship describing variation in transpiration and K_L