Water economy of Neotropical savanna trees: six paradigms revisited

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Summary   Biologists have long been puzzled by the striking morphological and anatomical characteristics of Neotropical savanna trees which have large scleromorphic leaves, allocate more than half of their total biomass to belowground structures and produce new leaves during the peak of the dry season. Based on results of ongoing interdisciplinary projects in the savannas of central Brazil (cerrado), we reassessed the validity of six paradigms to account for the water economy of savanna vegetation. (1) All savanna woody species are similar in their ability to take up water from deep soil layers where its availability is relatively constant throughout the year. (2) There is no substantial competition between grasses and trees for water resources during the dry season because grasses exclusively explore upper soil layers, whereas trees access water in deeper soil layers. (3) Tree species have access to abundant groundwater, their stomatal control is weak and they tend to transpire freely. (4) Savanna trees experience increased water deficits during the dry season despite their access to deep soil water. (5) Stomatal conductance of savanna species is low at night to prevent nocturnal transpiration, particularly during the dry season. (6) Savanna tree species can be classified into functional groups according to leaf phenology.

We evaluated each paradigm and found differences in the patterns of water uptake between deciduous and evergreen tree species, as well as among evergreen tree species, that have implications for regulation of tree water balance. The absence of resource interactions between herbaceous and woody plants is refuted by our observation that herbaceous plants use water from deep soil layers that is released by deep-rooted trees into the upper soil layer. We obtained evidence of strong stomatal control of transpiration and show that most species exhibit homeostasis in maximum water deficit, with midday water potentials being almost identical in the wet and dry seasons. Although stomatal control is strong during the day, nocturnal transpiration is high during the dry season. Our comparative studies showed that the grouping of species into functional categories is somewhat arbitrary and that ranking species along continuous functional axes better represents the ecological complexity of adaptations of cerrado woody species to their seasonal environment.

Keywords: cerrado, nighttime transpiration, tropical savannas, water deficit, water uptake.

Introduction

Before the first studies of water relations of Neotropical savannas, beginning in the 1940s (e.g., Ferri 1944, Valio et al. 1966, Goodland and Ferri 1979, Medina 1982, Sarmiento 1983, Sarmiento and Monasterio 1983, Goldstein et al. 1986), biologists had long been puzzled by the striking morphological, anatomical and phenological characteristics of savanna trees (Warming 1909). In the extremely seasonal environment of Neotropical savanna ecosystems, which are characterized by about five rainless months and a long period with high precipitation, woody species have large scleromorphic leaves that are renewed during the dry season. Most Neotropical savanna trees are evergreen, though a few species are leafless for a relatively short period. Many species allocate more than half of their biomass to belowground structures (Sarmiento 1983, Castro and Kauffman 1998). Fire is a conspicuous feature during the dry season, and the bark of savanna trees tends to be thick and insulating (Hoffmann et al. 2003). The deep and permeable savanna soils are oligotrophic, with low pH and high aluminum and iron contents (Furley and Ratter 1988). Adaptation to the particular features of the savanna environment has resulted in a number of unusual plant characteristics. Many hypotheses have been proposed to explain how savanna plants are adapted to the strong seasonal variation in precipitation and low soil nutrient availability (for a review on savanna

functional types based on leaf phenology see Eamus and Prior 2001). The objective of this review is to reevaluate six well established paradigms about the water relations of Neotropical savanna woody species in the light of recent findings.

Tropical savannas are the second most extensive vegetation type in South America, once covering more than 1.5 million km², the cerrado of central Brazil forming the largest regional system (Goodland 1971, Texeira de Oliveira-Filho et al. 1989). Cerrado communities are remarkably complex and are characterized by tree species diversity far greater than that of other Neotropical savanna regions (Sarmiento 1984). More than 500 species of tree and large shrub are present in savanna ecosystems (Ratter et al. 1996), and even relatively small areas may contain up to 70 or more species of vascular plant (Felfili et al. 1998). The principal factors influencing the structure of cerrado vegetation include a pronounced seasonality of precipitation, frequent fires, low soil fertility, high temperatures and low humidities (e.g., Hills 1969, Medina 1982, Cochrane 1989). The low relative humidity and high daytime temperatures in the cerrado impose a consistently high evaporative demand during the prolonged dry season. During the dry season, water in upper soil layers is severely depleted as evidenced by the dieback of grasses and by the low water potential in the upper portion of the soil profile (Franco 1998, 2000), whereas in deeper soil layers the water content remains high, even after several months without rain.

Strong vertical stratification in soil water availability provides the basis for the two-layer model of tree–grass coexistence in savanna ecosystems (Walker and Noy-Meir 1982, Knoop and Walker 1985). According to this model, the shallow roots of grasses make them superior competitors for water in the upper part of the soil profile, whereas deeply rooted woody plants have exclusive access to a more reliable water source in the lower part of the soil profile.

We considered this hypothesis with reference to the following six long-standing paradigms concerning the water relations of tropical savanna trees, focusing on recent results of ongoing interdisciplinary projects in the savannas of central Brazil (cerrado). (1) All savanna woody species are able to take up water from deep soil layers where its availability is relatively constant throughout the year. (2) There is no substantial competition between grasses and trees for water resources during the dry season because grasses explore upper soil layers exclusively, whereas trees are able to access water from deeper soil layers. (3) Because tree species have access to abundant groundwater, their stomatal control is weak and they transpire freely. (4) Savanna trees experience increased water deficits during the dry season despite their access to deep soil water. (5) Stomatal conductance (g_s) at night is low, preventing nocturnal transpiration, particularly during the dry season when water is less available. (6) Savanna tree species can be classified into distinct functional categories according to leaf phenology; i.e., deciduous, brevi-deciduous and evergreen.

Most data to assess the above paradigms were obtained at study sites in the Ecological Reserve of the Instituto Brasileiro de Geografia e Estatistica (IBGE), an experimental field station 33 km south of Brasília (15°56′ S, 47°53′ W, 1100 m a.s.l.). Mean annual rainfall is about 1500 mm, with a rainy season from October to March or April, and a long, nearly rainless dry season from early May to September. During the dry season, relative humidity reaches as low as 10% at midday. Nocturnal relative humidity during the dry season also tends to be low. Mean annual temperature is about 22 °C, with little seasonal variation. Several vegetation classification systems exist for cerrado structural types or physiognomies, based mainly on tree density. Here we emphasize three representative physiognomies: (1) cerradão, medium to tall woodlands with closed or semi-closed canopy; (2) cerrado sensu stricto, savanna woodland with low trees or shrubs and open canopy cover of about 50%; and (3) campo sujo, open savanna with scattered trees and shrubs. Results for nineteen dominant tree species occurring at the study sites are reviewed (Table 1). Only limited reference will be made to savanna studies outside of Brazil.

Results and discussion

1. Root systems of woody plants

Consistent with the two-layered model of tree–grass coexistence, it is assumed that most woody species of cerrado vegetation have deep roots that access constantly available water and that such roots are a prerequisite for maintaining high leaf water potentials (Ψ_l) during the dry season when most trees produce a new crop of leaves (Walter 1971, Sarmiento 1984). However, we have observed marked differences among woody species in their patterns of water uptake, with deciduous species tapping water from deeper soil layers than those accessed by evergreen species as indicated by comparing the stable hydrogen isotope composition (δD) of xylem sap and soil water at different depths during the dry season (Jackson et al. 1999), when evaporative fractionation near the soil surface creates a gradient of soil water δD with depth, with higher δD values near the soil surface to more negative values at depth. Mean δD values were −35‰ for the upper 100 cm of soil and −55‰ between 230 and 400 cm depth at our study site. Concurrent analyses of xylem and soil water δD values indicated a distinct partitioning of water resources among deciduous and evergreen species (Figure 1A). Five out of the eight evergreen species studied had a mean xylem water δD value of about −35‰, whereas xylem sap from deciduous species had a mean δD value of about −50‰. Among evergreen tree species, minimum Ψ_l was negatively correlated with xylem water δD, suggesting that access to more readily available water at greater depths permitted maintenance of a more favorable plant water status (Figure 1B). Even though the deciduous species are leafless for less than a month, direct measurements of sap flow in roots indicate that the relative contribution of tap roots to overall tree water economy is more substantial in deciduous cerrado trees than in evergreen cerrado trees (Scholz 2006).

These results are inconsistent with the idea that all woody species have similarly deep root systems. There are not only differences in the patterns of water uptake between deciduous and evergreen trees, but also species-specific differences

Table 1. Species and characteristics of individuals used in Figures 1–6. Source indicates references for previously published data.

Species	Family	Leaf phenology	External diameter (cm)	Height (m)	Source
Aspidosperma tomentosum	Apocynaceae	Deciduous	3.2–6.8	1.8–3.1	Scholz 2006
Byrsonima crassa	Malpighiaceae	Brevideciduous	4.7–10.3	1.5–2.3	Scholz 2006
Blepharocalyx salicifolius	Myrtaceae	Brevideciduous	5.5–10.2	2.8–4.5	Bucci et al. 2004*b*, 2005
Caryocar brasiliense	Caryocaraceae	Brevideciduous	8.7–11.1	2.6–4.1	Bucci et al. 2004*b*, 2005
Dalbergia miscolobium	Leguminosae	Brevideciduous	3.8–5.1	5.6–8.3	Jackson et al. 1999
Erythroxylum suberosum	Erythroxylaceae	Deciduous	3.5–4.7	1.7–1.8	Bucci et al. 2004*b*, 2005
Kielmeyera coriacea	Guttiferae	Deciduous	2.8–4.5	1.7–2.8	Bucci et al. 2004*b*, 2005
Miconia ferruginata	Melastomataceae	Evergreen	1.3–2.4	4.8–6.5	Jackson et al. 1999
Myrsine guianensis	Myrisnaceae	Evergreen	4.5–9.5	1.5–2.6	Unpublished data
Ouratea hexasperma	Ochnaceae	Evergreen	4.5–9.5	1.5–2.6	Bucci et al. 2004*a*, 2004*b*, 2005
Pterodon pubescens	Leguminosae	Brevideciduous	7.1–8.8	12.3–22	Jackson et al. 1999
Qualea grandiflora	Vochysiaceae	Deciduous	3.3–5.7	8.2–9.4	Jackson et al. 1999
Qualea parviflora	Vochysiaceae	Deciduous	3.1–6.9	2.9–4.5	Bucci et al. 2004*a*, 2004*b*, 2005
Roupala montana	Proteaceae	Evergreen	4.6–5.9	1.9–2.2	Meinzer et al 1999, Bucci et al. 2005
Schefflera macrocarpa	Araliaceae	Evergreen	4.5–8.8	2.7–4.4	Bucci 2001, Bucci et al. 2004*a*, 2004*b*
Styrax ferrugineus	Styracaceae	Evergreen	4.5–11.3	4.2–10	Bucci et al. 2004*a*, 2004*b*, 2005
Sclerolobium paniculatum	Leguminosae	Evergreen	12.3–15.6	6.5–8	Meinzer et al. 1999, Scholz 2006
Vochysia elliptica	Vochysiaceae	Evergreen	2.2–3.4	4.8–6.9	Jackson et al. 1999
Vochysia thyrsoidea	Vochysiaceae	Evergreen	9.2–12.0	6.3–7	Scholz 2006

among evergreen trees (Jackson et al. 1999). In addition to differences in patterns of water uptake among species, many trees have dimorphic root systems with both deep and shallow roots (see Paradigm 2). At a community level, this implies that trees are extracting water from the whole soil profile down to the water table during the wet season when soil water potentials (Ψ_s) remain close to 0 MPa, and that water uptake shifts to greater depths during the dry season as a consequence of declining water availability in the upper soil layers.

2. Competitive interactions between woody and herbaceous species

According to the two-layered model of tree–grass coexistence (Walker and Noy-Meir 1982, Sarmiento 1984), shallow-rooted grasses are superior competitors for water in the upper part of the soil profile, whereas woody plants have exclusive access to deeper and more abundant water sources. A corollary of this paradigm is that the two groups of species interact little despite their spatial proximity. Although there has been little work on competitive interactions between trees and grasses in Neotropical savannas, recent reviews of studies in other savannas (Scholes and Archer 1997, House et al. 2003) demonstrate considerable competition between trees and grasses. Therefore, we focus on recent observations that hydraulic lift links water use by herbaceous and woody plants, particularly during the dry season (Scholz et al. 2002, Moreira et al. 2003, Meinzer et al. 2004).

The movement of water from moist to dry portions of the soil profile via plant root systems has been termed hydraulic lift (Richards and Caldwell 1987, Caldwell and Richards 1989) or, more generally, as the movement of water may be in any direction (Burgess et al. 1998, 2001, Smith et al. 1999), hydraulic redistribution (Burgess et al. 1998). The process requires only a gradient in Ψ_s, a root system that explores soil layers with different water potentials, a more positive Ψ in the xylem of some of the roots than in surrounding dry soil layers and a low resistance to reverse flow of water from roots to soil. Hydraulic lift usually occurs at night when transpiration has diminished sufficiently to allow Ψ of the aboveground part of the plant and near surface roots to attain a higher value than the drier portions of the soil profile. It is believed that hydraulic redistribution contributes significantly to the water balance of both the plant responsible for it, and neighboring plants of other species (Dawson 1993, Moreira et al. 2003). Water released from roots into drier soil layers may be reabsorbed when transpiration exceeds water uptake by deep roots alone (Richards and Caldwell 1987). Furthermore, hydraulic redistribution may enhance nutrient uptake by fine roots located in the relatively nutrient rich upper portion of the soil profile, which normally undergoes severe desiccation during long dry seasons (Caldwell et al. 1998), and it may promote the activity of mycorrhizae and symbiotic nitrogen fixing bacteria as the bulk soil in the upper portion of the profile dries.

Our recent studies indicate that the cerrado region is characterized by the presence of many woody species with dimorphic
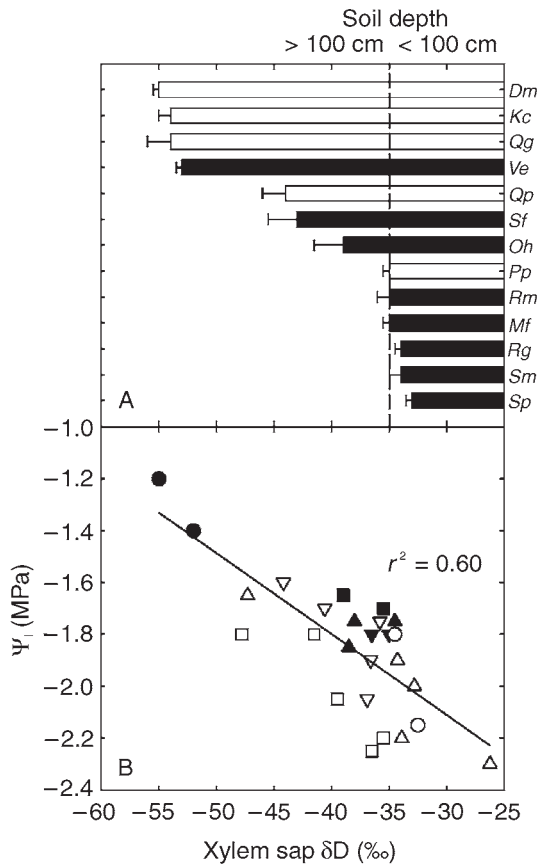
Figure 1. (A) Xylem sap stable hydrogen isotope composition (δD; ± SE, $n = 3–4$), near the end of the dry season for eight evergreen (filled bars) and five deciduous (open bars) woody cerrado species. Approximate limit of two distinct soil layers with different water δD is indicated by the vertical dashed line. (B) Minimum leaf water potential (Ψ_l) in relation to xylem sap δD for eight evergreen cerrado species. Each value represents a different individual: *Mf*, *Miconia ferruginata* (■); *Oh*, *Ouratea hexasperma* (▽); *Rg*, *Myrsine guianensis* (△); *Rm*, *Roupala montana* (▲); *Sm*, *Schefflera macrocarpa*, (▼); *Sp*, *Sclerolobium paniculatum* (○); *Sf*, *Styrax ferrugineus* (□); *Ve*, *Vochysia elliptica* (●); *Qp*, *Qualea parviflora*; *Pp*, *Pterodon pubescens*; *Qg*, *Qualea grandiflora*; and *Dm*, *Dalbergia miscolobium*. Data are from Jackson et al. (1999) and S.J. Bucci, unpublished data.

root systems (Scholz et al. 2002, Scholz 2006). We have studied the occurrence and magnitude of hydraulic redistribution in cerrado woody species during the dry season and the dry-to-wet season transition (Scholz et al. 2002, Moreira et al. 2003, Meinzer et al. 2004, Scholz 2006). All woody species with dimorphic root systems that were studied exhibited hydraulic redistribution. For example, the tap root of *Byrsonima crassa* Nied. exhibits positive flow (toward the shoot) during the day and almost zero flow at night (Figure 2). However, shallow roots often exhibit positive flow during the day and reverse flow (to the soil) at night (Figure 2, insert). The coexistence of many species with different rooting and soil water uptake patterns (see Paradigm 1) and the redistribution of soil water by roots suggest that soil water partitioning and its dynamics in the cerrado are more complex than predicted by the
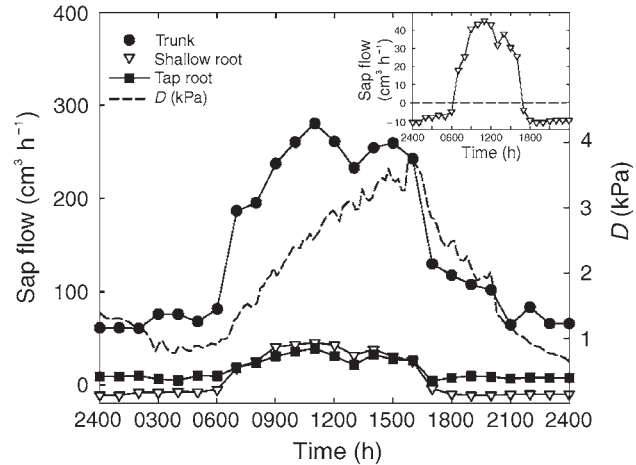

Figure 2. Sap flow in the main trunk, a shallow root (5 to 10 cm depth) and a tap root of a *Byrsonima crassa* tree measured at the IBGE research station in central Brazil during the dry season. Inset shows sap flow of a shallow root with an expanded scale depicting nighttime reverse flow. All sap flow measurements were made with heat pulse systems (Burgess et al. 2001, Scholz et al. 2002). The individual studied had new fully expanded leaves. Soil water potential was –1.7 MPa at 10 cm (depth of shallow root) and –0.6 MPa at 100 cm. Air saturation deficit (D) during the measurement day is shown. Data adapted from Scholz 2006.

two-layered model.

In a recent study using both the heat pulse method and isotopic (deuterium) labeling, we observed that water hydraulically lifted to the upper soil layer by deep-rooted trees was used by neighboring plants including other woody and herbaceous species (Moreira et al. 2003). Water lifted to surface soil layers by tree roots is insufficient to sustain physiological activity of herbaceous plants throughout the dry season (Moreira et al. 2003, Scholz 2006), but it may be sufficient to mitigate loss of hydraulic function in shallow roots of woody species during the dry season (Domec et al. 2004, 2006). Such interactions between deep and shallow roots of woody species are inconsistent with the independent behavior of woody and herbaceous plants of Neotropical savannas as predicted by the two-layered model, as has been found true of other savanna types throughout the world (e.g., Scholes and Archer 1997, Espeleta et al. 2004, Ludwig et al. 2004).

3. Stomatal behavior of savanna woody species

In early studies relying on rapid weighing of detached leaves, Ferri (1944) concluded that many cerrado trees transpire freely throughout most of the year, although a few species restrict transpiration at the end of the dry season. Subsequent studies have confirmed the general absence of seasonal restriction of transpiration (e.g., Goodland and Ferri 1979). The putatively weak stomatal control of transpiration in cerrado trees was explained by continuous access to water stored deep in the soil (Ferri 1944, Goodland and Ferri 1979). At the stand level, Miranda et al. (1997) reported substantial reductions in both leaf area index and evapotranspiration during the dry season at

a cerrado sensu stricto site. However, eddy flux measurements do not distinguish between water losses from woody and from herbaceous plants. It is known that herbaceous plants with relatively shallow root systems die back during the dry season and this could explain the dry season decrease in ecosystem evapotranspiration. Additional measurements with open-top chambers or photosynthesis measurement systems help to quantify the contribution of total evapotranspiration from the understory vegetation layers (Hutley et al. 2000, authors' unpublished results).

In a study on the regulation of whole-plant water use in four dominant evergreen tree species at the IBGE research station, Meinzer et al. (1999) observed that strong stomatal limitation of maximum daily transpiration rates and total daily transpiration was evident during both wet and dry seasons. Sap flow typically increased in the morning, attained a maximum value by about 0930–1030 h, and then decreased sharply despite increasing solar radiation and atmospheric evaporative demand. Despite partial defoliation in many species, which helps maintain high leaf specific conductivity during the dry season, g_s is lower in the dry season than in the wet season (see Paradigm 4). A substantial decrease in the plant's gas exchange surface should result in higher g_s under similar air saturation deficit (D) conditions. In another study (Bucci 2001), *Schefflera macrocarpa* Seem. (D.C. Frodin) showed similar patterns of stomatal regulation, with a rapid increase in g_s and sap flow early in the morning and a sharp decline in both long before air saturation deficit peaked in the afternoon (Figure 3). Finally, Domec et al. (2006) reported a linear decline in daily maximum g_s with increasing native embolism in shallow roots of four cerrado woody species during the dry season.

These results are inconsistent with the assumption that woody savanna species exercise weak stomatal control of transpirational losses. Water use by cerrado woody plants is limited by a combination of physiological, plant architectural and tree density constraints. Hydraulic limitations are imposed on the amount of water that can be extracted and transpired daily by cerrado trees and shrubs. In addition, total evapotranspiration and the proportion of evapotranspiration associated with water taken up at depth is further limited by low woody plant density. We suggest that use of precipitation by cerrado vegetation increases along a gradient of increasing tree density. Recent results indicate that stand-level water utilization is proportional to tree basal area along a gradient in tree density from campo sujo to cerradão and that canopy conductance is lower during the dry season (Bucci et al. unpublished results).

4. Tree water deficits during the dry season

Shallow-rooted herbaceous species die back during the 4- to 5-month-long savanna dry season while woody plants remain physiologically active. Some savanna woody species experience increased water deficits during this period, others maintain relatively high Ψ_l throughout the dry season (Perez and Moraes 1991, Medina and Francisco 1994). Our recent studies suggest that most cerrado species in central Brazil are isohydric (Franco 1998, Meinzer et al. 1999, Bucci et al. 2005),
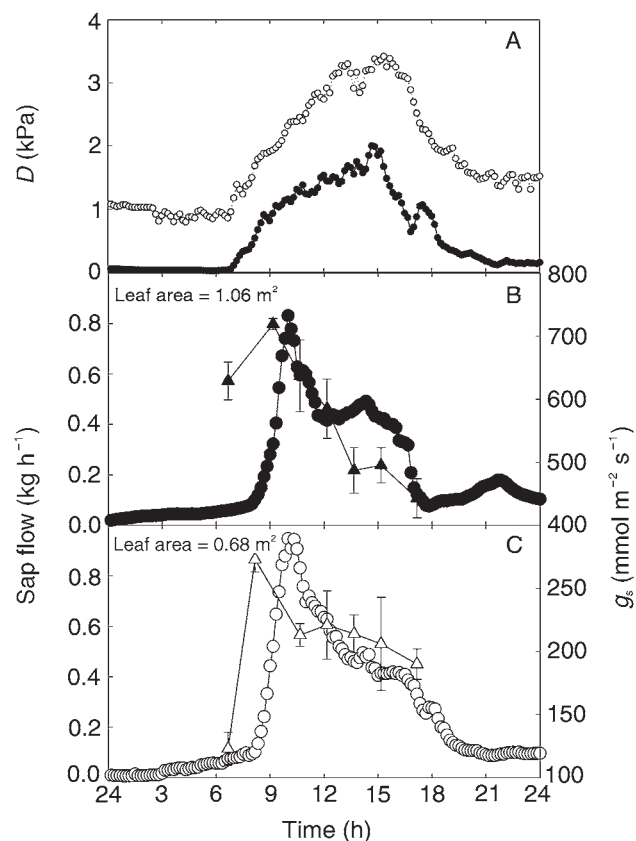
Figure 3. (A) Air saturation deficit (*D*) during typical dry (○) and wet (●) season days. Typical daily courses of sap flow (●, ○) and stomatal conductance (g_s; ▲, △) during the (B) wet and (C) dry seasons in a dominant evergreen cerrado species (*Schefflera macrocarpa*) at the IBGE research station in central Brazil. Total leaf area per tree during sap flow measurements is shown in each panel. All measurements of sap flow were made by the heat dissipation method (Granier 1985, 1987). Stomatal conductance was measured with a steady-state porometer. Data adapted from Bucci 2001.

maintaining nearly constant minimum Ψ_l throughout the year, despite changes in soil water availability and atmospheric conditions (Tardieu and Simmoneau 1998). Some mechanisms that contribute to homeostasis in Ψ_l have been outlined by Whitehead (1998). For example, when the air saturation deficit increases, a concomitant decrease in g_s or total leaf surface area can limit transpiration, thereby constraining variation in minimum Ψ_l. However, if the leaf-specific conductance of the soil–leaf pathway increases, g_s should increase, as long as the air saturation deficit and total leaf surface area remain constant (Whitehead 1998). Such coordination between the gas phase and liquid phase conductance appears to be universal (e.g., Meinzer and Grantz 1990, Lloyd et al. 1991, Meinzer el al. 1999, Comstock 2000, Meinzer 2002).

The mechanisms contributing to homeostasis of minimum Ψ_l in Neotropical savanna trees have not been fully studied. We have recently shown that the isohydric behavior of cerrado tree species throughout the year results from strong daytime stomatal control of transpiration, a decrease in total leaf surface area per tree during the dry season and tight coordination

between gas and liquid phase conductance (Bucci et al. 2005). Figure 4A shows minimum Ψ_l during the rainy and dry seasons for 13 cerrado species. The differences in Ψ_l were not statistically significant at $P < 0.1$ for 11 of the 13 species studied. In contrast, daytime g_s and total leaf surface area per plant were typically lower during the dry season (Figures 4B and 4C). In one species, *Blepharocalyx salicifolius* (H.B. & K.) Berg., leaf surface area per individual was not significantly different between wet and dry seasons, however, daytime g_s differences between seasons were larger than in any other species studied. The preceding results are inconsistent with claims that Neotropical savanna woody species experience increased water deficits during the dry season. Despite species-specific differences in rooting depths, most tree species exhibit a similar minimum Ψ_l during both the wet and dry seasons. In contrast, tree seedlings may be less able to maintain homeostasis in Ψ_l. Their roots tend to be restricted to upper soil layers during the first years of life and, therefore, do not have access during the dry season to available water in deeper soil layers (Franco 2002). In a recent study, Hoffmann et al.

Figure 4. (A) Midday leaf water potentials (Ψ_l); (B) mean stomatal conductance (g_s); and (C) total leaf area per tree during the wet (filled bars) and dry (lined bars) seasons for the representative cerrado woody species listed in Table 1. Bars are means + 1 SE. Measurements were made on three to five leaves per tree (A and B) and two to five trees per species (all panels). Measurements were obtained with a pressure chamber and a steady-state porometer. Data obtained from Bucci et al. 2004*a*, Bucci et al. 2005 and Scholz 2006.

(2004) reported that predawn leaf water potential (Ψ_{pd}) of seedlings of three cerrado tree species closely tracked Ψ_s at 15 cm depth. As a result they reached Ψ_{pd} of -2 to -4 MPa, which is substantially lower than values measured in adult trees during the dry season.

5. Nighttime stomatal opening

It has been proposed that stomata tend to minimize transpiration relative to photosynthetic carbon gain and balance transpiration rates with the efficiency of water supply to the leaves (Cowan and Farquhar 1977, Sperry 2000). According to optimization theory, non-CAM plants have low g_s at night to prevent transpirational water loss. Negligible or low nocturnal transpiration is assumed to allow Ψ_l and Ψ_s to equilibrate before dawn, with the result that Ψ_{pd} can serve as a surrogate for Ψ_s (Ritchie and Hinckley 1975, Hinckley et al. 1978, Richter 1997). However, if nighttime transpiration prevents equilibration along the soil-to-leaf continuum, Ψ_{pd} may be significantly more negative than the Ψ_s (Donovan et al. 1999, 2001). An estimate of Ψ_s is necessary to calculate the driving forces of water movement along the soil–plant–atmosphere continuum. Information on nighttime transpiration may help to assess if equilibration along this continuum occurs before dawn. Despite its importance, there is little information on the relationship between nocturnal water loss and Ψ_{pd} disequilibrium between soil and leaves in tropical trees. The assumption that g_s is low at night applies to all plants, but is particularly relevant for cerrado trees because of the high nocturnal evaporative demand that prevails during the long dry season in cerrado ecosystems.

Nocturnal transpiration has been studied in relatively few species, because it is commonly assumed that stomata are closed at night or that water vapor near leaf surfaces is at or near saturation, or both. However, studies with temperate woody species indicate that, under certain environmental conditions, nocturnal water loss can be substantial (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). At cerrado sites, nighttime values of relative humidity as low as 40 to 50% are frequent during the dry season and could result in substantial nocturnal transpiration if stomata are not completely closed.

Tree stems function both as pathways for long-distance water transport and as water storage compartments. Internal water storage in cerrado trees is large and plays an important role in maintaining adequate water balance (Scholz et al. 2007*a*). When Ψ_l falls as transpiration increases in early morning, water moves from storage into the transpiration stream, helping to minimize temporal imbalances between water supply and demand, and temporarily slowing the decline in Ψ_l. Water stored in stem tissues can contribute from 6 to 50% of the total water lost 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 usually occurs during late afternoon and at night when evaporative water loss is low, but it can occur during the daytime if leaf-to-air
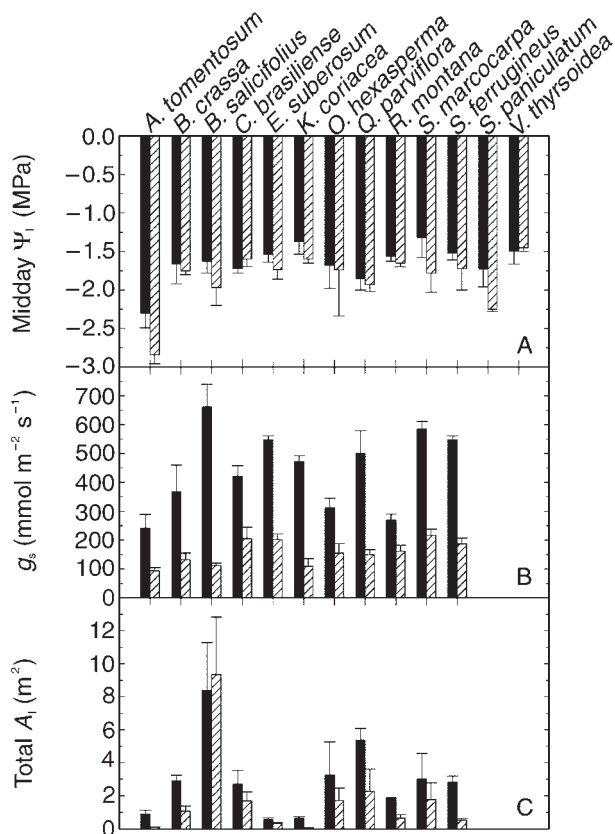
vapor pressure difference is small (Goldstein et al. 1998). Nocturnal transpiration may prevent the complete recharge of internal water storage compartments of cerrado trees (Bucci et al. 2004a, Scholz et al. 2007a), decreasing the water available internally and consequently limiting the supply of water to transpiring leaves at the beginning of the next day. A complete rehydration of stem water storage compartments is a prerequisite for overnight equilibration of Ψ_l with Ψ_s.

It has been found that nocturnal g_s never dropped below 50 mmol m^{-2} s^{-1} in three dominant cerrado tree species (Figure 5A). Consistent with the observed nocturnal g_s, nocturnal sap flow was substantially higher in exposed trees than in trees covered with plastic bags (Figure 5B). Preventing nocturnal transpiration by enclosing the foliage in plastic bags resulted in 0.25 to 0.50 MPa increases in nighttime Ψ_l compared with freely transpiring trees, confirming that nocturnal transpiration is an important factor preventing equilibration between Ψ_s and Ψ_l (Figure 5C). These results refute the idea that stomata

of Neotropical savanna woody species are tightly closed at night. Furthermore, nocturnal transpiration may be adaptive in cerrado trees. Continuous water use at night may enhance nutrient uptake from nutrient-poor cerrado soils and speed nutrient transport to aboveground plant parts. Nocturnal transpiration during the dry season does not result in the same water loss as daytime transpiration, because evaporative demand is lower at night. In a recent study of Brazilian cerrado trees growing in unfertilized plots and plots to which nitrogen and phosphorus had been added twice yearly from 1998 to 2005, it was found that nocturnal sap flow was lower in the fertilized plots than in the unfertilized plots (Scholz et al. 2007b). Nocturnal g_s was also lower in fertilized plots than in unfertilized plots, and nocturnal Ψ_l was more negative in the unfertilized plots. These results are consistent with the idea that nocturnal transpiration is of adaptive value in nutrient-poor ecosystems subjected to seasonal drought.

6. Tree functional groups

Since the late 1970s, a common approach in plant ecology has been to assign plants to functional groups or types (e.g., Grime 1979, Pearcy and Ehleringer 1984). The aim being to simplify complex ecosystems and their interactions by dealing with a tractable number of plants characterized by shared functional traits rather than with individual species. The members of one functional group should differ consistently from those of another group in a single trait or set of traits or responses. A functional trait commonly used for grouping tropical tree species is leaf phenology (e.g., evergreen, brevideciduous or deciduous). The underlying assumption is that, regardless of identity, species within each group respond similarly to particular types of environmental perturbation, but that responses will differ among groups. Plant biology literature has many examples of contrasting species- or functional, group-specific behaviors or ecological characteristics affecting basic physiological processes such as transpiration, photosynthesis and growth. However, traditional concepts of plant functional groups are currently being reevaluated in view of apparent global convergence among numerous plant functional traits that has emerged from analyses of large datasets that include information on diverse species (e.g., Reich et al. 1997, Niklas and Enquist 2001, Wright et al. 2004). By functional convergence we mean that the same "rule" or "set of rules" can be used to scale relationships between functional and structural or morphological traits of a diverse group of organisms. In addition, species-specific resource allocation patterns at the individual level often result in enhancement of a particular function at the expense of another, particularly in resource-limited environments, such as tropical savannas with low water and nutrient availability. Examples of these trade-offs include enhancement of water-use efficiency at the expense of nitrogen-use efficiency (Field and Mooney 1983) and the negative association between leaf lifespan and photosynthesis (Reich et al. 1997, Cordell et al. 2001). Conflicting allocation of resources tends to constrain the number of possible combinations of functional traits in a particular individual and among species, leading to functional convergence across a broad range of spe-
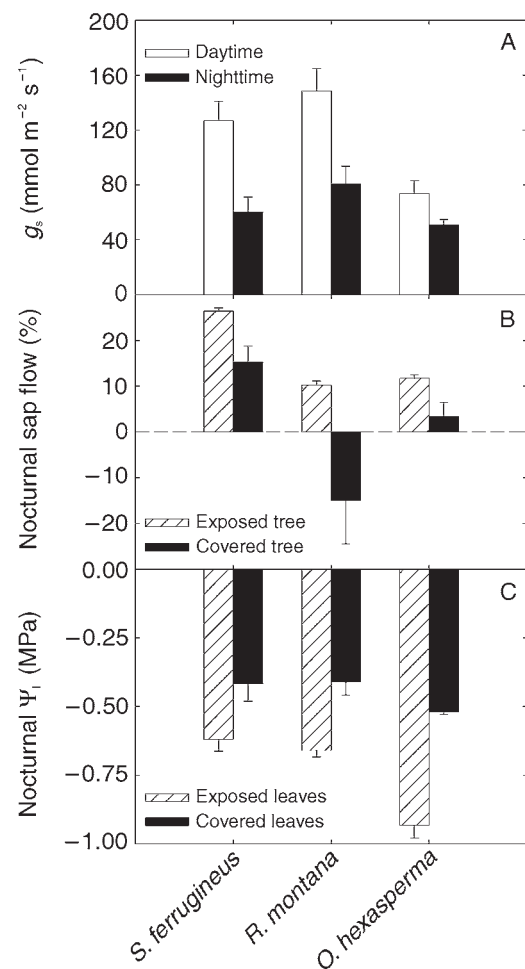

Figure 5. (A) Diurnal and nocturnal mean stomatal conductance (g_s), (B) nocturnal sap flow of exposed and covered trees and (C) nocturnal leaf water potential (Ψ_l) of exposed and covered leaves of three dominants evergreen cerrado woody species. Bars are means + 1 SE of six leaves for Ψ_l, ten leaves for g_s and 4 days of sap flow measurements. Data obtained from Bucci et al. 2004a.

cies (Schulze et al. 1994, Reich et al. 1997, Meinzer 2003, Bucci et al. 2004*b*).

Examples of functional convergence among water relations traits of several evergreen and deciduous savanna species are depicted in Figure 6. The diurnal range of Ψ_l was negatively related to leaf specific hydraulic conductivity (k_l), suggesting that higher water transport efficiency constrained variation in Ψ_l. Functional convergence was also observed when g_s was plotted against the ratio of leaf to sapwood area (A_l:A_s), an allometric surrogate of K_l. The variables utilized in Figure 6 reflect traits linked to overall plant performance. The use of appropriate variables, strongly related to overall plant fitness, to scale variation in physiological traits among species may reveal functional similarities that cannot be detected with measurements at smaller scales (Meinzer 2003). These and other functional relationships reported for cerrado woody species (Bucci et al. 2004*b*, 2005, Franco et al. 2005) are better descriptors of successful trait syndromes and of trade-offs than discrete plant functional types, because the evergreen, deciduous and brevideciduous functional types overlap substantially
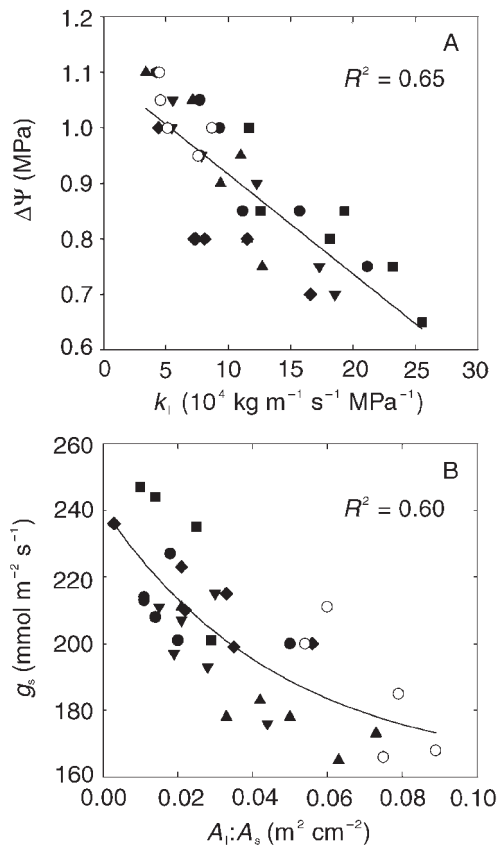
in allometric relationships among ecophysiological characteristics. This suggests that grouping of species by functional type is somewhat arbitrary and that formulations of plant functional typologies that represent variation along a continuum may better represent the ecological complexity resulting from the adaptations of cerrado woody species to their environment. The study of continuous variation in ecophysiological traits offers a means of describing the effects of changes in species composition on ecosystem structure and function that may result from climate change or changes in groundwater depth, which would likely shift the favorable operating ranges of functional traits along universal scaling relationships

Conclusions

We have presented and analyzed empirical evidence to test six paradigms concerning the water economy of savanna vegetation and have shown that observed trait variability is inconsistent with these models. The existence of large species-specific differences in the patterns of water uptake between deciduous and evergreen trees and among evergreen tree species have profound implications for regulation of tree water balance. Water lifted to upper soil layers by deeply rooted woody plants and the patterns of water uptake by woody species with dimorphic root systems are both inconsistent with the independence of woody and herbaceous plants that is assumed by the two-layered savanna model. We provide evidence of strong stomatal control of transpirational losses and show that adults of most tree species exhibit year round homeostasis in Ψ_l. In addition, we observed that nocturnal transpiration is relatively high during the dry season, that the assignment of species to functional groups is somewhat arbitrary and that formulations of plant functional typologies which represent variations along a continuum may better represent the ecological complexity of adaptations of cerrado woody species to their seasonal environment.

Figure 6. (A) Diurnal variation in leaf water potential ($\Delta\Psi_l$) in relation to leaf specific hydraulic conductivity (k_l) and (B) stomatal conductance (g_s) in relation to leaf area per unit sapwood area (A_l:A_s) for six of the cerrado tree species listed in Table 1. Each value represents one individual of one species: *Schefflera macrocarpa* (▲); *Styrax ferrugineus* (●); *Kielmeyera coriacea* (■); *Ouratea hexasperma* (▼); *Caryocar brasiliense* (◆); and *Erythroxylum suberosum* (○) ($n = 6$ for all species). Data obtained from Bucci et al. 2004*b*.

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