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Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees

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Abstract Water availability is a principal factor limiting the distribution of closed-canopy forest in the seasonal tropics, suggesting that forest tree species may not be well adapted to cope with seasonal drought. We studied 11 congeneric species pairs, each containing one forest and one savanna species, to test the hypothesis that forest trees have a lower capacity to maintain seasonal homeostasis in water relations relative to savanna species. To quantify this, we measured sap flow, leaf water potential (Ψ_L), stomatal conductance (g_s), wood density, and Huber value (sapwood area:leaf area) of the 22 study species. We found significant differences in the water relations of these two species types. Leaf area specific hydraulic conductance of the soil/root/leaf pathway (G_t) was greater for savanna species than forest species. The lower G_t of forest trees resulted in significantly lower Ψ_L and g_s in the late dry season relative to savanna trees. The differences in G_t can be explained by differences in biomass allocation of savanna and forest trees. Savanna species had higher Huber values relative to forest species, conferring greater transport capacity on a leaf area basis. Forest trees have a lower capacity to maintain homeostasis in Ψ_L due to greater allocation to leaf area relative to savanna species. Despite significant differences in water relations, relationships between traits such as wood density and minimum Ψ_L were indistinguishable for the two species groups, indicating that forest and savanna share a common axis of water-use strategies involving multiple traits.

Keywords Leaf area index · Huber value · Sap flow · Brazil · Cerrado

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Introduction

Species traits play an undeniable role in mediating individual and species-level responses to the environment (Westoby et al. 2002). Therefore, where traits are shared by many species in a particular vegetation type, they can influence the distribution of that biome. This is an implicit assumption of many dynamic vegetation models that seek to predict global biome distributions by simulating the response of a limited number of representative plant functional types (Tang and Bartlein 2008). Understanding the influence of species traits on vegetation distribution is especially important in the tropics where species diversity

is high and land-use patterns pose an imminent threat to the distribution of natural habitats.

Savanna and evergreen forest are the two most extensive biomes in the tropics, yet there is no consensus regarding the factors that determine their distributions. Characteristics of species such as water relations and allocation patterns may play a particularly important role here, as suggested by the nature of savanna-forest boundaries. Many savanna-forest boundaries are characterized by a sharp transition in both vegetation structure (Bowman 2000; Hennenberg et al. 2005) and species composition (Hoffmann et al. 2009). Typically, few tree species are common to both tropical savanna and forest environments (Adejuwon and Adesina 1992; Felfili and da Silva 1992), suggesting that savanna and forest species play distinct roles in vegetation structure and response to environment.

In the Cerrado region of Brazil, there are many consistent differences between savanna and forest species. Forest species are taller (Hoffmann et al. 2003), have greater growth rates and larger crowns (Rossatto et al. 2009), higher specific leaf area (Hoffmann et al. 2005) and are more susceptible to fire than savanna species (Hoffmann et al. 2009). In the absence of fire, forest tree species commonly expand into savanna, but rates of canopy closure are slow (San José and Fariñas 1991; Durigan and Ratter 2006), suggesting that other factors also limit the rate of forest expansion. Water availability is an important factor governing tree survival in savanna, and therefore has likely exerted strong natural selection on species traits in these seasonal habitats. Although mean annual precipitation can vary widely throughout tropical savannas, a distinct dry season is characteristic of these habitats (Bond 2008). In the dry season, low rainfall and high evaporative demand pose a potential barrier to species not adapted to these conditions.

In the Brazilian cerrado, where the current study was undertaken, savanna species rely on a suite of traits and behaviors to cope with water deficit in the dry season. Deep roots give savanna trees access to ample soil water (Oliveira et al. 2005; Kelley et al. 2007), and as much as 80% of water transpired in the dry season originates from depths below 1 m (Oliveira et al. 2005). Furthermore, savanna trees avoid excessive transpirational losses through strong controls over stomatal conductance (g_s) and/or leaf area (Bucci et al. 2005). These characteristics, combined with sufficient capacity for water transport, allow savanna species to avoid substantial declines in water potential during the dry season despite maintaining high rates of transpiration (Bucci et al. 2005). It is unknown whether forest tree species possess these same traits and behaviors that allow savanna species to ameliorate the effects of water deficit. Relative to savanna species, seedlings of forest species tend to have lower investment in root mass (Hoffmann and Franco 2003); this trend appears to continue through adulthood, as indicated by a compilation of ecosystem-level studies (Castro and Kauffman 1998). However, equivalent comparisons of stomatal behavior, regulation of leaf water potential (Ψ_L) and efficiency for water transport are lacking (but see Hao et al. 2008).

In this study we compare the water relations of adult savanna and forest trees growing in the savanna environment. We test the hypothesis that forest trees exhibit a lower capacity to maintain homeostasis of water relations relative to savanna species, which ultimately may have a large impact on the distribution of gallery forests (i.e., forests that grow near watercourses) in the seasonal tropics. We expect that forest trees will have lower (more negative) Ψ_L and/or g_s in the dry season, compared to savanna trees living in the same environment. We also expect that the apparent leaf-area specific hydraulic conductance of the soil/root/leaf pathway (G_t) will be lower for forest trees due to a higher ratio of leaf area to sapwood area. To test this hypothesis and to determine whether the water relations of forest trees may limit their expansion into neighboring savannas, we contrast the water relations of 11 congeneric species pairs, each containing one species typical of the savanna environment and another found primarily in adjacent gallery forests. Fire has been suppressed at the study site for >30 years; as a result forest species have begun to colonize the savanna, making it possible to contrast the water relations of these species types under similar environmental conditions.

Materials and methods

Study site and plant material

The study site was located in the cerrado of central Brazil at the Reserva Ecológica do IBGE (the Brazilian Institute of Geography and Statistics) approximately 30 km from Brasília (15°56′S, 47°53′W, 1,100 m altitude). Average annual precipitation is 1,500 mm and there is a pronounced dry season from May until September. Daily minimum humidity ranges from 33 to 97% in the wet season, and from 16 to 58% in the dry season (values taken from a meteorological station installed near study sites). The soils are deep, well-drained oxisols.

Vegetation of the cerrado region is heterogeneous, consisting of a gradient of tree density from open grassland (campo limpo) to dense woodlands (cerradão), and a diversity of forest types including gallery (riparian) forests and upland forests ranging in phenology from evergreen to deciduous. This study took place in savanna sites that had approximately 50% tree cover (locally known as cerrado sensu stricto) where, following >30 years of fire

Table 1 Species information for the congeneric pairs included in this study

Genus name	Specific epithet	Authority	Family	Habitat	Phenology
Byrsonima	*pachyphylla*	Griseb. (=*B. crassa* Nied.)	Malpighiaceae	Savanna	Evergreen
Byrsonima	*laxiflora*	Griseb.	Malpighiaceae	Forest	Evergreen
Guapira	*noxia*	(Netto) Lundell	Nyctaginaceae	Savanna	Deciduous
Guapira	*areolata*	(Heimerl) Lundell	Nyctaginaceae	Forest	Evergreen
Machaerium	*opacum*	Vogel	Fabaceae (Faboideae)	Savanna	Deciduous
Machaerium	*acutifolium*	Vogel	Fabaceae (Faboideae)	Forest	Deciduous
Miconia	*pohliana*	Cogn.	Melastomataceae	Savanna	Evergreen
Miconia	*cuspidata*	Naudin	Melastomataceae	Forest	Evergreen
Myrcia	*tomentosa*	(Aubl.) DC.	Myrtaceae	Savanna	Deciduous
Myrcia	*rostrata*	DC.	Myrtaceae	Forest	Evergreen
Myrsine	*guianensis*	(Aubl.) Kuntze [=*Rapanea guianensis* (Aubl.) Kuntze]	Myrsinaceae	Savanna	Evergreen
Myrsine	*ferruginea*	Spreng. Or (Ruiz and Pav.) Spreng.	Myrsinaceae	Forest	Evergreen
Ouratea	*hexasperma*	(A.St.-Hi) Baill.	Ochnaceae	Savanna	Evergreen
Ouratea	*castaneaefolia*	(DC.) Engl.	Ochnaceae	Forest	Evergreen
Qualea	*parviflora*	Mart.	Vochysiaceae	Savanna	Deciduous
Qualea	*dichotoma*	Warm. ex Wille	Vochysiaceae	Forest	Brevi-deciduous
Schefflera	*macrocarpa*	(Cham. and SchltdL) Seem.	Araliaceae	Savanna	Evergreen
Schefflera	*morototonii*	(Aubl.) Decne. and Planch.	Araliaceae	Forest	Evergreen
Styrax	*ferrugineus*	Nees and Mart.	Styracaceae	Savanna	Evergreen
Styrax	*camporum*	Pohl	Styracaceae	Forest	Evergreen
Vochysia	*thyrsoidea*	Pohl	Vochysiaceae	Savanna	Evergreen
Vochysia	*tucanorum*	(Spreng.) Mart	Vochysiaceae	Forest	Evergreen

suppression, forest species have established, allowing us to study savanna and forest species growing in a common savanna environment.

We focused our study on 11 congeneric species pairs, each containing a species typical of savanna and another typical of forest (for phenology and taxonomic information see Table 1). The forest species included in this study are all common in well-drained portions of gallery forest areas well upslope from water courses as well as in savanna sites protected from fire. Elsewhere, most, if not all, of these species are also found in upland mesophytic forests in the region (Oliveira-Filho and Ratter 1995). Both deciduous and evergreen trees at this site often experience a reduction in leaf area throughout the dry season [S. G. Gotsch, personal observation and leaf area index (LAI) data, this study]. Deciduous trees often maintained at least partial canopies until late in the dry season. We studied five individuals of each species. To avoid site bias for comparisons of savanna and forest species, we chose five locations throughout the reserve where it was possible to study both species of a genus in close proximity. In most cases, all individuals of both congeneric species were located in the same site, while in a few cases, individuals were distributed over two or three sites (but always with representatives of both congener species at each site).

Four to six pairs of soil psychrometers (PST-55; Wescor, Logan, Utah) were installed at depths of 30 and 70 cm and were uniformly distributed throughout each of the five sites. Soil water potential was measured in the late wet season, the middle of the dry season and at the end of the dry season using a dew point microvoltmeter (model HR-33T; Wescor). Soil water potential was measured on the same day in all sites. ANOVA did not detect differences in soil water potential across the sites in any season (effect of site: wet season, $F = 0.55$, $P = 0.7$; mid-dry, $F = 0.39$, $P = 0.75$; late dry $F = 0.87$, $P = 0.49$).

Sap flow

Sap flow was measured on three to five trees per species using the constant heating method (Granier 1985, 1987) and was conducted at the end of the wet season (April) and the middle of the dry (July) seasons of 2007 and 2008. Each sap flow probe was constructed from a pair of 20-mm-long (1.5-mm-diameter) hollow steel needles. Each needle contained a copper-constantan thermocouple and a constantan heating element. The heating element on the

upper needle was supplied with a current that allowed for 0.2 W of heat dissipation. Probes were placed 10 cm apart and were inserted approximately 30 cm from ground level. Molding clay was placed around the external portion of the probes which was then covered with aluminum foil. The clay served as insulation and the foil was used to reflect sunlight which could alter the temperature of the probes. Probes were left for 24 h prior to being connected. Voltage differences between the two probes were measured every 30 s, averaged every 10 min and then stored in a CR1000 datalogger (Campbell Scientific), which was connected to an AM 16/32 or AM 416 Multiplexer (Campbell Scientific).

Since species were measured in a number of sites throughout the reserve it was not possible for all trees to be measured concurrently. All species were measured over 4 consecutive weeks in the wet and dry seasons, and both members of a species pair were measured at the same time. Trees of a range of diameters were used, but special care was taken to include the largest possible trees in a site. Trees with diameters under 5 cm were not used for sap flow. Sap flow stations ran long enough to capture at least 1 full sunny day (usually 5 days) in each site. After the 5-day period, the current to the heating element was disconnected, while measurements were continued for 48 h to record natural temperature gradients between the probes. We used these measurements to adjust sap flow calculations (Lundblad et al. 2001).

Sap flow was calculated using a standard empirical relationship (Granier 1985, 1987). Mass sap flow was calculated by multiplying the sap flow by the cross-sectional area of the active xylem. We estimated sapwood area from empirical relationships between diameter at 30 cm and sapwood area determined from five to ten trees of each species. We drilled a hole 30 cm from ground level in the main stem (at a 45° angle) and injected safranin dye (0.1%). After 4 h, an increment borer was used to extract a core perpendicular to the stem about 2 cm above the previous hole; sapwood was then identified from the presence of stain on the core (R. Villalobos, unpublished method). The equations were then used to estimate the sapwood area for the sap flow trees (r^2 ranged from 0.7 to 0.98, $P < 0.01$; for most species r^2 was above 0.85).

The apparent leaf-area specific conductance of the soil/root/leaf pathway (G_t) was determined as

$$G_t = E/\Delta\Psi$$

where $\Delta\Psi$ is the difference between the midday Ψ_L and the soil water potential (estimated here by predawn bagged leaf water potential) and E is the midday transpiration rate per unit leaf area determined from sap flow measurements. Leaf area was estimated by multiplying the average LAI for the species by the projected area of the individual tree crown. The projected crown area was estimated with the formula for the area of an ellipse (A_e):

$$A_e = \pi(0.5X) \times (0.5Y)$$

where X is the longest length of the canopy and Y is the width measured perpendicularly to X.

LAI was measured in the wet and dry seasons for each species with a digital plant canopy imager CI-110 (CID) at dawn, dusk, or on cloudy days. LAI was measured on sap flow trees whenever possible, but it was not always possible to obtain an unimpeded view of the crown, preventing LAI measurements. Instead we used an average LAI determined from six to 16 trees of the same species, depending on the availability of acceptable subjects and the variation in the LAI within species.

Leaf water potential

Ψ_L was measured concurrently with the sap flow measurements in the wet and mid-dry seasons of 2007 and 2008. Ψ_L was also measured at the end of the dry season (late September) to obtain measures of the minimum Ψ_L (Ψ_{min}). Ψ_L was measured on all five study trees of each species. Leaves were collected between 5:00 and 6:30 a.m. for predawn measurements and between 11:30 a.m. and 1:00 p.m. for midday measurements. Four leaves per tree were covered with aluminum foil and sealed in a plastic bag the afternoon prior to predawn measurements. Leaves were bagged to stop transpiration in order to obtain an estimate of the average predawn soil water potential at the root zone. Nocturnal transpiration has previously been observed in these savannas late in the dry season (August and September), which would result in biased estimates of sap flow and soil water potential (Bucci et al. 2004). This is not likely to have had an influence in the current study, since nighttime dew formation is prevalent in July, indicating that there was not a sufficient vapor pressure gradient to sustain transpiration. Leaf wetness sensors (Decagon Devices, Pullman, Wash.) installed nearby indicated that dew formation occurred on all but 4 nights in July 2008; equivalent data are not available for 2007. Ψ_L was taken on the second full day of sap flow measurements. Eight leaves were collected for the predawn measurements (four covered and four uncovered), while four sun leaves were collected for midday measurements. Leaves were removed from branches within different areas of the canopy with a razor blade. Each leaf was placed in a sealable plastic bag with a small piece of humid paper towel and placed in a cooler with ice. After all leaves were collected they were brought back to the lab and measured immediately using a pressure chamber (Plant Moisture Systems, Corvallis, Ore.). A minimum of two bagged and two unbagged leaves were measured per tree; when there was a

discrepancy in the measurements, the additional collected leaves were measured.

Stomatal conductance

Midday g_s was measured on five trees of each of the species at the end of the wet season, the middle of the dry season, and the end of the dry season using an AP4 steady-state porometer (Delta-T, Cambridge, England). g_s was measured on the same day as Ψ_L. In most cases we used the same trees that were in use for the other water relations measures, but occasionally this was not possible due to the height of the trees. In this case we substituted nearby individuals for these measurements. g_s was measured on three or four sun leaves per tree that were at different cardinal locations. The youngest fully expanded mature leaf on a branch was measured on all trees to ensure similar leaf ages.

Wood density

To determine wood density, a 5- to 6-cm section of a branch was split, the bark and pith removed, and the sapwood fresh volume was determined using the water displacement method. Wood density was measured on ten to 17 individuals (one branch per individual) per species depending on the availability of individuals. The segment was then dried for 72 h at 60°C and weighed.

Analyses

Ψ_L, soil water potential, and g_s were analyzed using repeated-measures ANOVA. The effects of time (predawn, midday), genus (random factor), species type (savanna, forest), and season (late wet, mid-dry, late dry) were tested in the analysis for Ψ_L. Site was not included as a factor in the analysis for Ψ_L or g_s since both species of a genus were found within the same site. Site and depth were the effects tested for soil water potential. Species type and season were the only effects in the analysis for g_s, since this measurement was only taken at midday. Differences in G_t for savanna and forest species were analyzed using a mixed model two-way ANOVA. The effects in this analysis were genus (random factor) and species type (fixed factor). G_t was analyzed separately in the wet and dry seasons.

We used linear regression to test for significant correlations between Ψ_L, g_s, and G_t, and Huber value (sapwood area:leaf area). In cases where a significant correlation was detected, we used analysis of covariance (ANCOVA) to test for differences between savanna and forest species in the slope and intercept of the relationship. All data were log-transformed prior to analyses to achieve normality; Ψ_L values were multiplied by −1 before log transforming since

these values are negative. In addition to using an ANOVA to test for an effect of season on Ψ_L of savanna and forest trees, t-tests were performed on the species means to test for differences between savanna and forest trees from season to season for predawn and midday values. Finally, a principal components analysis (PCA) was performed on all multivariate trait data measured in this study, to examine patterns of covarying traits of savanna and forest species. Traits that were not normally distributed were log-transformed; a varimax rotation was used on the loadings. All analyses were completed using JMP version 7.0 (SAS Institute, Cary, N.C.) except for the mixed model ANOVAs which were analyzed using SAS version 9.1 (SAS Institute).

Results

Ψ_L was significantly more negative in forest than savanna species occupying the same site (Fig. 1a). Repeated-measures ANOVA showed significant effects of species type
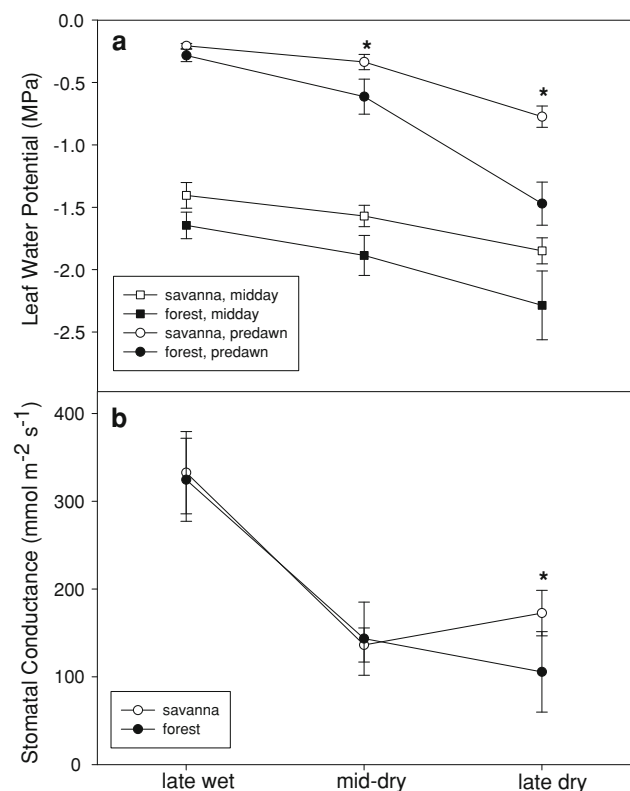

Fig. 1 **a** Leaf water potential and **b** stomatal conductance from the end of the wet season until the end of the dry season 2007. There was a significant effect of species type, season, and time of day for leaf water potential but not for stomatal conductance. *Error bars* indicate SEs. *$P \leq 0.05$ [significant differences between species type (savanna vs. forest) at the time of measurement (predawn, midday, late wet, mid-dry, late dry)]

($F = 5.65$, $P = 0.0245$), season ($F = 101.39$, $P < 0.0001$), and time of day ($F = 124.29$, $P = 0.0001$), while all interactions were non-significant. Wet-season predawn [−0.2 savanna (S) vs. −0.28 MPa forest (F), $t = 1.323$, $P = 0.10$] and midday (−1.4 S vs. −1.64 MPa F, $t = 1.598$, $P = 0.06$) Ψ_L were similar for both species types. By the end of the dry season, forest species had more negative predawn and midday Ψ_L than savanna species although when tested separately this difference was only significant for predawn Ψ_L (predawn, −0.77 S vs. −1.47 MPa F, $t = 2.03$, $P = 0.03$; midday, −1.84 S vs. −2.2 MPa F, $t = 1.105$, $P = 0.14$). Furthermore, in the late dry season, the difference between predawn and midday Ψ_L was significantly greater in the savanna species relative to forest species ($F = 7.61$, $P = 0.007$, genus as random factor) indicating a smaller driving force for water movement through the forest species late in the dry season. Midday g_s declined for both savanna and forest species from the wet season to the middle of the dry season ($F = 19.61$, $P = 0.002$; Fig. 1b). When tested across all sample dates, neither species type ($F = 2.35$, $P = 0.169$) nor genus ($F = 1.32$, $P = 0.3633$) had a significant effect on g_s. In the late dry season, however, the g_s of savanna species was greater than that of forest species (172.6 S vs. 105.65 F mmol m^{-2} s^{-1}, $t = 3.09195$, $P = 0.0025$).

The Huber value was significantly greater for savanna than forest species ($F = 18.16$, $P < 0.0001$; Fig. 2a). When tested within pairs, this difference was significant for eight of 11 genera (*t*-tests, *Byrsonima* $P = 0.038$, *Guapira*

$P = 0.0003$, *Miconia* $P = 0.0003$, *Myrcia* $P = 0.03$, *Myrsine* $P < 0.0001$, *Ouratea* $P < 0.0001$, *Styrax* $P = 0.0015$, *Vochysia* $P = 0.0001$). There was no significant difference in Huber values between species of *Qualea*, *Machaerium* and *Schefflera* (Fig. 2a).

The G_t was significantly greater for savanna species than for forest species in both the wet and dry seasons (wet, $F = 19.04$, $P < 0.0001$; dry, $F = 3.92$ $P = 0.05$). The effect of genus was significant in both seasons (wet, $F = 7.59$, $P < 0.0001$; dry, $F = 8.23$ $P < 0.0001$), as was the interaction between species type and genus (wet, $F = 1.96$ $P = 0.048$; dry, $F = 3.54$ $P = 0.0008$). For five of the 11 genera, when examined within species pairs, savanna species had a significantly greater value of G_t than their forest congener (*t*-tests, *Byrsonima* $P = 0.04$, *Guapira* $P = 0.004$, *Styrax* $P = 0.0097$, *Vochysia* $P = 0.0049$, *Myrcia* $P = 0.02$). Four additional species exhibited the same pattern, though the differences were not significant (*t*-tests, *Ouratea* $P = 0.06$, *Miconia* $P = 0.07$, *Qualea* $P = 0.3$, *Myrsine* $P = 0.09$), and only one genus (*Schefflera*) showed the reverse pattern (Fig. 2b).

Both predawn and midday (Fig. 3a) Ψ_L were negatively correlated with wood density and there was no significant difference in the slopes or intercepts of these relationships between savanna and forest species. The correlation between wood density and midday Ψ_L was weakest in the wet season ($r^2 = 0.31$, $P = 0.01$) and was strongest at the end of the dry season ($r^2 = 0.733$, $P < 0.0001$). This strengthening of the correlation corresponded to a progressive increase in the slope of the relationship as the dry season progressed. Similarly, the relationship between wood density and predawn Ψ_L became increasingly stronger with increasing drought conditions, being non-significant in the wet season ($r^2 = 0.07$, $P = 0.2$), but increasing in the middle ($r^2 = 0.23$, $P = 0.02$) and at the end ($r^2 = 0.54$ $P = 0.001$) of the dry season.

Relationships between wood density and Ψ_{min} (lowest Ψ achieved during the dry season), midday g_s and G_t, as well as between Huber value and Ψ_{min}, midday g_s and G_t, were tested using ANCOVA, linear regression, and pairwise correlation coefficients. The ANCOVA results indicate that savanna and forest species did not have significantly different slopes in the aforementioned relationships. The regressions were calculated with both savanna and forest species together and habitat types are indicated in Fig. 3a–f. Ψ_{min}, lowest g_s achieved during the dry season (g_{smin}) and G_t were all negatively correlated (Table 2) with wood density ($P < 0.0001$, $P = 0.001$, $P = 0.0026$, respectively). The relationship was strongest between wood density and Ψ_{min} ($r^2 = 0.73$) and weakest (but significant) between wood density and G_t ($r^2 = 0.22$). Huber value was positively correlated with Ψ_{min}, g_{smin}, and G_t ($P = 0.0254$, $P = 0.0005$, $P < 0.0001$, respectively). A strong
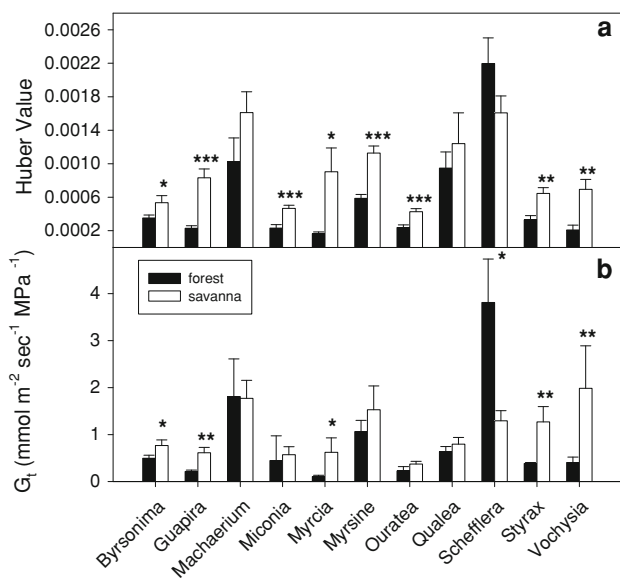

Fig. 2 a Huber value (sapwood area:leaf area) and **b** apparent leaf-area specific hydraulic conductance of the soil/root/leaf pathway (G_t) of savanna and forest congeneric species. *Error bars* represent SEs. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

Fig. 3 Correlations between dry season leaf water potential, stomatal conductance, G_t and wood density (**a**–**c**), or Huber value (**d**–**f**). For all correlations the *line* represents the linear regression between the two variables. The slopes of the trait relationships for savanna and forest trees did not significantly differ from one another, thus, relationships are shown using a single regression line. Abbreviations comprise the first two letters of the genus name followed by the first two letters of the specific epithet (see Table 1 for full names): *four-letter uppercase codes* indicate savanna species, *four-letter lowercase codes* indicate forest species
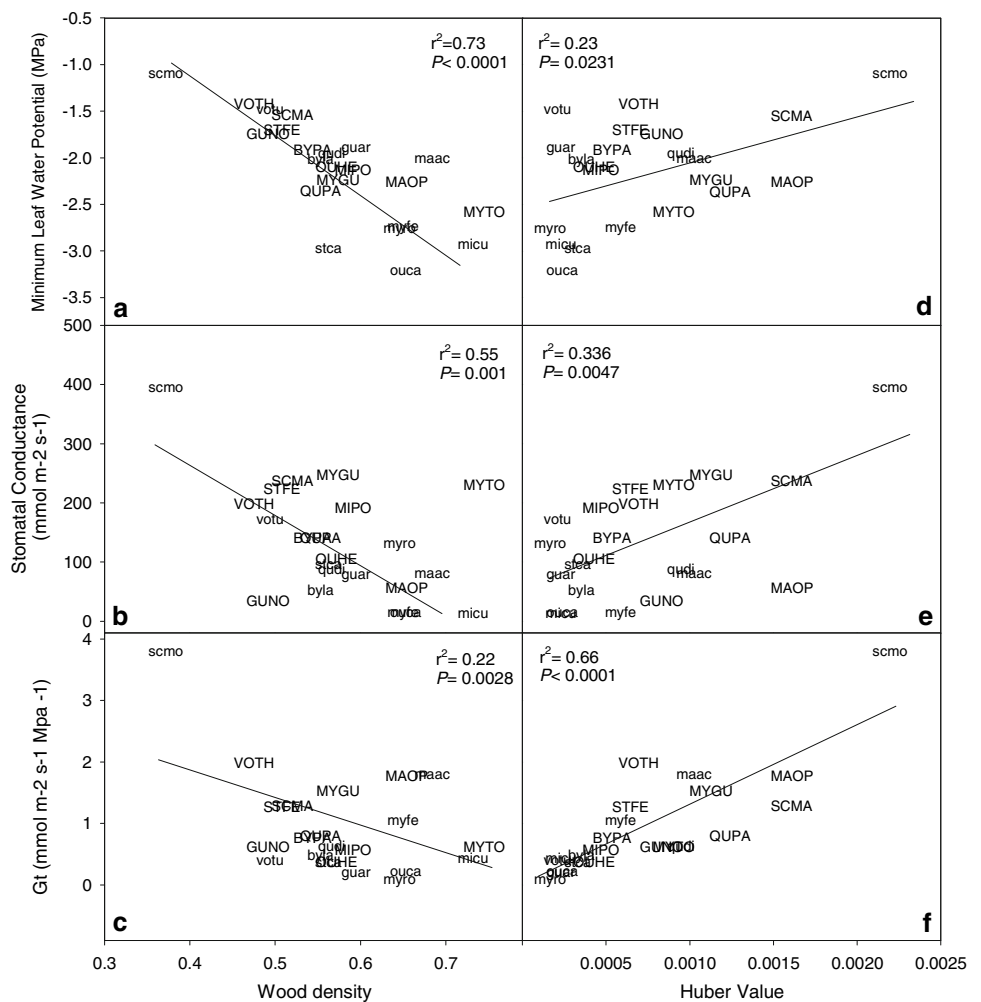
Table 2 Pairwise correlation matrix for wood density, water relations and allocation traits (correlation coefficients calculated from species averages)

	LWP	g_s	WD	H	G_t	LAI	ST	MT	MF
LWP		−0.729	0.892	−0.459[†]	−0.602	n.s.	−0.489[†]	−0.520	0.538
g_s	−0.729		−0.721	0.665	0.549	−0.493[†]	0.602	0.488[†]	n.s.
WD	0.892	−0.721		n.s.	−0.415	n.s.	−0.595	n.s.	n.s.
H	−0.459[†]	0.665	n.s.		0.819	−0.706	0.494	0.531	n.s.
G_t	−0.602	0.549	−0.415	0.819		−0.688	0.408[†]	0.444	n.s.
LAI	n.s.	−0.493[†]	n.s.	−0.706	−0.688		n.s.	−0.509	n.s.
ST	−0.489[†]	0.602	−0.595	0.494	0.408[†]	n.s.		n.s.	−0.42[†]
MT	−0.52	0.488[†]	n.s.	0.531	0.444	−0.509	n.s.		n.s.
MF	0.538	n.s.	n.s.	n.s.	n.s.	n.s.	−0.42[†]	n.s.	

All values significant at $P < 0.05$ unless otherwise indicated; † significant trend ($P < 0.055$), *n.s.* not significant

Traits were log10 transformed and then analyzed using JMP version 7.1 for Windows; for LWP, the correlation coefficients were calculated using log transformations of the positive values

LWP Minimum leaf water potential, g_s midday late dry season stomatal conductance, *WD* wood density, *H* Huber value, G_t apparent leaf-area specific conductance of the soil/root/leaf pathway, *LAI* leaf area index, *ST* start time of sap flow, *MT* time of maximum sap flow, *MF* midday flow rate

relationship was detected between the Huber value and G_t ($r^2 = 0.66$) and between G_t and LAI ($r^2 = 0.44$).

The first two axes of the PCA explained 45.1 and 16.7% of the variation in the nine traits (Fig. 4a). The first axis was defined primarily by midday dry season g_s, Ψ_{min}, wood density, and the time of day of maximum sap flow (Fig. 4b). Position along this axis was not strongly related to species type. In contrast, along PCA axis 2 there was a strong shift in the position of savanna species, relative to forest species. This shift along axis 2 is attributed to the

Fig. 4 Position of forest and savanna species (**a**) and traits (**b**) on the first two axis of the principal components analysis for all the traits included in this study. Both forest and savanna species were spread evenly along the first axis, while these groups were separated along the second axis. For abbreviations, see Table 2

lower LAI, higher Huber value, and higher G_t of savanna species.

Discussion

Differences in the water relations of savanna and forest trees

As expected, the efficiency for water transport, quantified as G_t, was generally greater for savanna species than for forest species. The lower G_t of forest species has the inevitable consequence of lower daytime values of g_s and/ or Ψ_L, owing to the direct functional relationships among transpiration, Ψ and G_t. Both g_s and Ψ were lower among forest species, although this difference was significant only at the end of the dry season. The higher mean G_t among savanna species, relative to forest species, can be readily explained by differences in allocation. Of particular importance here is the greater Huber value exhibited by savanna species, which corresponds to a greater investment in water transport capacity per unit of leaf area. A greater Huber value in savanna species is likely the result of differences in allocation to leaf area. Savanna species consistently have lower leaf area than their forest congeners which causes the investment in sapwood area per leaf area to be higher in comparison with forest species.

While high G_t may be a necessary condition for homeostasis of water relations, maintaining high g_s and Ψ_L also requires deep roots with access to ample water during the dry season. Although rooting depths of our study species are not known, there is strong evidence that savanna species should have deeper root systems. Seedlings of savanna species have greater investment in root biomass than forest species and maintained higher predawn leaf water potentials (Hoffmann et al. 2004), while ecosystem-level comparisons indicate a greater ratio of belowground biomass: aboveground biomass (Castro and Kauffman 1998). However, there may not be a strong relationship between root biomass and rooting depth, since roots of tropical forest trees can extend to depths of many meters (Nepstad et al. 1994).

Stomatal regulation plays a particularly important role for maintaining homeostasis of Ψ_L in cerrado trees (Meinzer et al. 1999). By closing stomata as air vapor pressure deficit increases, transpiration is restricted, thereby preventing excessive declines in Ψ_L. Forest trees do exhibit a larger decrease in g_s in the late dry season, relative to savanna species, but this does not appear to be sufficient to avoid a decline in Ψ_L (Fig. 1a, b). Despite reductions in g_s of forest trees, we found significant differences in the Ψ_L of savanna and forest trees at the end of the dry season. Furthermore, forest species exhibited a
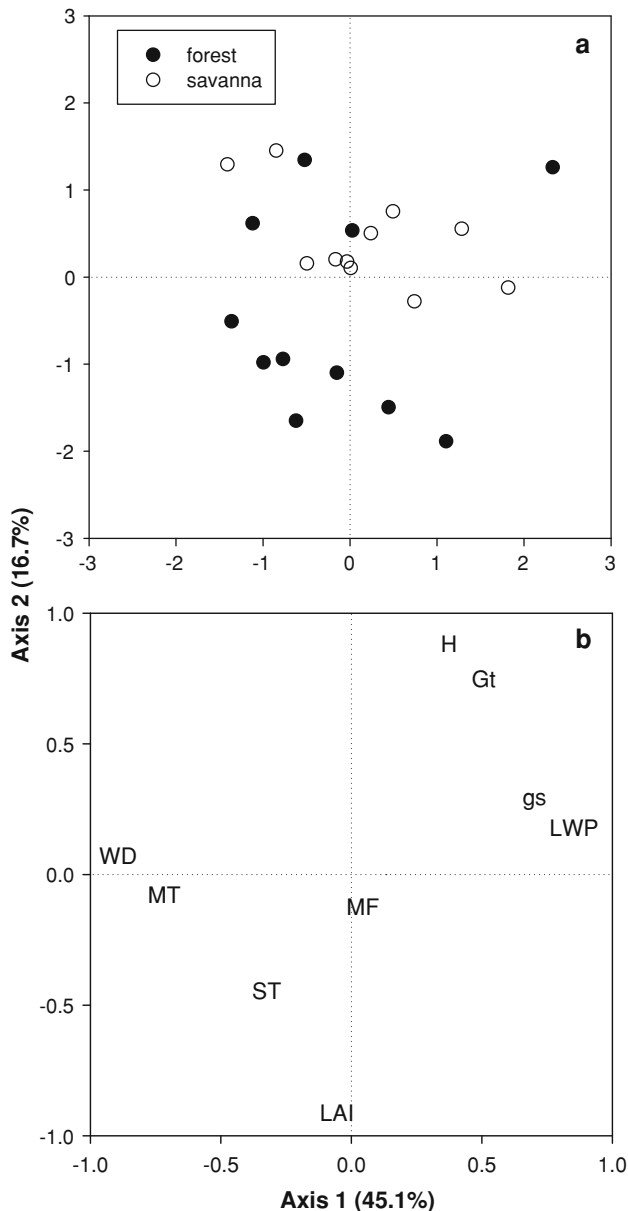
significantly smaller difference between predawn and midday Ψ, indicating a disparity in the driving forces of water transport in savanna and forest trees. Smaller driving forces in forest trees living in the savanna may limit the potential for water uptake, especially in dry years or if climate change causes reductions in rainfall in central Brazil.

The forest trees monitored in the present study probably established sometime after fire suppression was initiated in the 1970s. This allowed savanna and forest species to be compared under similar growing conditions. These species probably invaded from nearby gallery forests, where these species are common in well-drained portions of the forest. Most, if not all, of these species are also common in upland mesophytic and semideciduous forests of central Brazil. Other species in the gallery forests, however, are restricted to perennially wet soils, and appear not to readily expand into savanna (da Silva Jr et al. 1996). Even among the relatively drought-tolerant forest species studied here, the rate of encroachment into savanna has been slow; despite ∼35 years of fire suppression at the study site, forest species still account for a small fraction of tree stems in the savanna. Our results suggest that a seasonal reduction in water availability likely contributes to the slow rate of forest expansion because of the impact on g_s and consequently carbon balance. Despite the clear differences in the structure of savanna and forest trees, differences in g_s of the two groups were modest and significantly different only at the end of the dry season. Curiously, however, a recent study including many of the same species studied here has shown that forest trees living in the savanna had higher growth rates than savanna species (Rossatto et al. 2009). This suggests that reduced investment in roots and conducting tissue among forest species, while precluding homeostasis of water relations, is amply compensated by the higher growth rates afforded by increased allocation to photosynthetic tissue. Regardless, it is likely that the allocation patterns of forest species may play a more limiting role in water relations in years of extreme drought or early in plant development.

Trait relationships in savanna and forest trees

Despite enormous diversity in strategies of water use among plant species, there is mounting evidence of a common axis of variation involving multiple traits that relate to water use. At one extreme are species exhibiting a strategy of tolerance of water deficit, and possess high wood density, low Ψ_{min}, low hydraulic efficiencies, and high resistance to xylem cavitation (Ackerly 2004; Bucci et al. 2004). These species, generally referred to as "drought resistant" or "tolerant", may rely primarily on xylem structural features to avoid embolism (Meinzer et al.

2009). The combination of high wood density and low Ψ_{min} appears to have evolved as an adaptive strategy enabling trees to avoid high levels of embolism, stomatal closure and ultimately shoot death (Bhaskar et al. 2007; Davis et al. 2002). The construction costs associated with drought resistance are likely to result in a trade-off consisting of reduced efficiency of water transport and stem water storage capacity under well-watered conditions (Stratton et al. 2000; Meinzer 2003). At the other extreme of this spectrum are species that tend to avoid extreme water deficits and are characterized by low wood density, high Ψ_{min}, high hydraulic efficiencies and low resistance to xylem cavitation (Ackerly 2004; O'Grady et al. 2009). These species may also have greater reliance on stored water to minimize fluctuations in xylem tension (Meinzer et al. 2009). Such species are generally drought deciduous, deep rooted, or limited to sites with high water availability. However, trees with less dense wood have an advantage under well-watered conditions due to a greater capacity to store and transport water (Stratton et al. 2000; Meinzer 2003; Bucci et al. 2004; Gartner and Meinzer 2005).

In this study, significant correlations were found between wood density and Ψ_{min}, g_s and G_t (Fig. 3a–c) for both savanna and forest trees. Despite differences in mean values of some traits between savanna and forest trees, trait relationships were not significantly different for the two groups. This suggests that the tradeoffs and constraints that give rise to this common axis of variation do not differ between savanna and forest species.

Savanna and forest trees share the same relationship between wood density and Ψ_{min}, and there is large interspecific variation in traits, especially for forest trees. Large trait variation across forest species may be the result of greater niche partitioning in this habitat. In the gallery forest, there are shade-intolerant pioneer species and shade-tolerant climax species which are expected to have distinct species traits. Wood density has been shown to be correlated not only with water relations traits but with growth rates (Enquist et al. 1999); species with denser wood tend to have slower growth rates and greater longevity than species with lower wood density (Castro-Diez et al. 1998; Enquist et al. 1999). Climax species generally have greater longevity than pioneer species, therefore the variation in traits related to wood density in forest trees may result from the relationship between wood density and successional status, which will in turn affect how these trees respond to water availability. Although most forest species had high wood density relative to savanna species, *Schefflera morototonii,* a pioneer forest species has a very low wood density, high g_s, high Ψ_{min}, high Huber value (Fig. 2) and is relatively shade intolerant and fast growing (Myster and Walker 1997; Tyree et al. 1991). Savanna trees, in contrast, do not appear to show such clear specialization into pioneer

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