Leaf tissue water relations and hydraulic properties of sclerophyllous vegetation on white sands of the upper Rio Negro in the Amazon region

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(*Accepted 24 February 2009*)

Abstract: The objective of this study was to explore the leaf tissue water relations in terminal branches, as well as the relations between xylem structure and function of five sclerophyllous species coexisting on white sands within the Amazon region. In these species, which possess costly leaves and thrive in an extremely nutrient-poor habitat, the preservation of leaf survival would be of comparable importance to the preservation of xylem vessels. Three trees per species were tagged in the field for all measurements. Minimum leaf water potential (Ψ) was -1.53 ± 0.61 and -0.94 ± 0.10 MPa during rainless and rainy days, respectively. The Ψ for turgor loss averaged -1.92 ± 0.05 MPa. Therefore, minimum Ψ was maintained within a safety range above the critical value for turgor loss. Xylem (K_x) and leaf (K_l) specific conductivity averaged 1.4 ± 0.22 and 0.00033 ± 0.000045 kg m^{-1} s^{-1} MPa^{-1}, respectively. Water supply was favoured in species with higher vessel density, and all species depended on relatively less abundant larger vessels for water transport. This would be advantageous because leaves were unable to develop very negative water potentials in order to maintain transpiration. High transpiration rates may be restricted to a few hours daily so as to prevent cavitation of widest vessels.

Key Words: bana, *Catostemma sancarlosianum*, cell elasticity, *Heteropterys* sp., hydraulic sufficiency, *Pachira sordida*, *Remijia morilloi*, *Retiniphyllum concolor*, Venezuela, wood anatomy

INTRODUCTION

Low-stature tree species growing on white sands in areas of the upper Rio Negro inhabit and thrive in areas near the Equator, with a typical tropical humid climate and soils with very low nutritional status (Bongers *et al.* 1985, Herrera *et al.* 1978). These species exhibit a range of sclerophylly index values between 3.4 and 7.4 g crude fibre g^{-1} protein, which is related to their high C/N ratio, as a consequence of the limitation of N and P required for growth (Sobrado 2008, 2009; Sobrado & Medina 1980). Thus, leaf blades are very expensive to construct and maintain, both on dry-mass and leaf-area bases (Sobrado 2009). The significance of sclerophyllous leaves in species thriving in humid tropical environments with aseasonal rainfall seems to be longevity enhancement rather than drought tolerance (Turner 1994). The short- and long-term leaf water use efficiency for carbon assimilation is relatively low in these species (Sobrado 2008, 2009). However, stomata are fully open only in the early morning, and they close from late morning onwards (Medina *et al.* 1990, Sobrado 1977). Adjustment in stomatal aperture as air humidity decreases has been attributed to hydraulic constraints and is a mechanism to regulate water status (Meinzer *et al.* 1999, 2008; Sperry *et al.* 1988a, 2002). If the xylem leaf water potential is very low, this can lead to runaway embolisms which would decrease long-term water supply to leaves (Tyree & Sperry 1988). Thus, the maintenance of a maximally efficient hydraulic system would require that stomata close in order to regulate water loss in an appropriate fashion as the evaporative demand increases, so as to prevent xylem embolisms (Bond & Kavanagh 1999, Jones & Sutherland 1991, Saliendra *et al.* 1995, Sperry *et al.* 2002).

The ecological trend in vessel characteristics suggests that in warm and moist tropical habitats the xylem tissue consists of wider conduits (Baas 1986, Carlquist 1988). Long-distance water transport is much more efficient in wide vessels, which are also more vulnerable to embolisms. In fact, vessel cavitation has been related to interconduit pit diameters, which may increase linearly with vessel diameter (Hacke *et al.* 2006). Therefore, a

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xylem tension causing 50% loss of hydraulic conductivity is positively related to vessel diameter within the same species (Tyree *et al.* 1994). Across species, pit membrane characteristics may vary independently of vessel size resulting in lack of relationship between vessel diameter and cavitation resistance (Choat *et al.* 2008). Vessel diameter tends to decrease in terminal branches, which represents a substantial hydraulic constraint in trees (Tyree & Ewers 1991, Zimmermann 1983). Thus, leaves should be able to develop an increasing water potential gradient to draw water as the water transport becomes insufficient. Nevertheless, this may lead to reduced leaf turgor and photosynthesis, and can cause xylem dysfunction (Tyree & Sperry 1988). Reduction in the leaf water potential for turgor loss by lowering osmotic potential, as well as changes in elasticity, would allow the development of a large leaf-soil gradient for water uptake. Leaf pressure-volume analysis provides important parameters of leaf water relations; namely, relative water potential, osmotic potential and turgor pressure as a function of relative water content, as well as bulk elastic modulus (Richter 1997, Turner 1981, Tyree & Hammel 1982). This approach has been widely used to characterize plants thriving in contrasting environments as well as to assess the effect of stressing environmental conditions on adjustments to leaf water relations.

Leaf tissue characteristics reflect species adaptation to the dynamic changes in water status occurring under field conditions, and may be related to stem hydraulic sufficiency as well. However, the associations between leaf water-relation characteristics and xylem water transport have been less studied, particularly in tropical environments (Choat *et al.* 2007). The objective of this study was to explore the leaf tissue water relations in terminal branches, as well as the relations between xylem structure and function of five species coexisting on white sand areas at the upper Rio Negro. In these species, which possess costly leaves and thrive in an extremely poor habitat, the preservation of leaf survival would be of comparable importance to the preservation of xylem vessels.

METHODS

Study site

Within upper Rio Negro basin (North Amazon), distinctive forest ecosystems have been associated to differential soil characteristics and topographical conditions (Breimer 1985, Herrera 1977, Herrera *et al.* 1978). The tallest, most diverse and complex 'tierra firme' forests thrive on well-structured oxisols on slightly more elevated areas. The valleys with sandy spodozols are occupied by the 'Amazon caatinga' complex. Within these

sandy areas, slightly more elevated domes have very low nutrient availability and a fluctuating water table. This zone represents an extreme stressful environment and the vegetation is known locally as 'bana' (Bongers *et al.* 1985). The tops of the domes, know as open bana, are covered by 18 woody species 2–5 m tall, sparsely distributed. The open bana is the specific vegetation on white sands where this research was conducted. A more detailed description of this type of vegetation can be found elsewhere (Bongers *et al.* 1985, Sobrado 2009). The studied bana is located 11 km from San Carlos de Rio Negro (Amazonas, Venezuela; 1° 54′N; 67° 03′W) within the upper Rio Negro basin. The climate in this area is very wet, with an annual rainfall of 3500 mm, with no month having less than 100 mm precipitation, and mean temperature of 26.2 °C. Several ecophysiological studies have been performed previously in this open bana (Bongers *et al.* 1985, Medina *et al.* 1978, Sobrado 1977, 2008, 2009; Sobrado & Medina 1980).

Study species

The species selected were: *Catostemma sancarlosianum* Steyerm. (Malvaceae), *Heteropterys* sp. (Malpighiaceae), *Pachira sordida* (R. E. Schult.) W. S. Alverson (syn. *Rodognaphalopsis discolor* A. Robyns) (Malvaceae), *Retiniphyllum concolor* (Spruce ex Benth.) Müll. Arg. (Rubiaceae) and *Remijia morilloi* Steyerm. (Rubiaceae). These species coexist at the site, and their importance value index (IVI; Müller-Dombois & Ellenberg 1974) is highest for the dominant species *P. sordida* (IVI = 17%), intermediate for the co-dominant species *R. morilloi* (IVI = 12%) and *C. sancarlosianum* (IVI = 10%), and lowest in *Heteropterys* (IVI = 8%) and *R. concolor* (IVI = 5%). All these species possess thick leaf blades of comparable density, as well as a low N and P concentration (Sobrado 2008, 2009; Sobrado & Medina 1980). Sclerophylly index (crude fibre/crude protein) is about 7.2 ± 0.8 in *C. sancarlosianum* and *P. sordida*, and 3.9 ± 0.3 in the other three species (Sobrado 2009). A total of three trees per species were tagged for all measurements. Given the small size of these trees, the amount of harvested tissue was kept to a minimum so as to preserve the trees.

Leaf water relations

Minimum tree water status was characterized by measuring midday leaf water potential (Ψ, MPa) under contrasting conditions, after 8 rainless days (November 2007) and during rainy days (January 2008). The Ψ was measured with a pressure chamber (PMS, Model 1400) in one or two twig samples per tree per species.

Previous measurements of Ψ in these species were made in 1976–1977 (Sobrado 1977). Pressure-volume (P-V) curves were determined on randomly selected twigs from the tagged trees bearing 4–6 leaves. On the afternoon of the day prior to measurements, the selected twigs were bagged to allow maximal rehydration during night-time. This procedure avoids the problems associated with the rehydration of cut branches (Kubiske & Abrams 1990). The following day, bagged twigs were cut and transported indoors for measurements. Four to six twigs per species were allowed to dehydrate naturally on the laboratory bench and P-V curves were constructed. The dehydration of the twigs proceeded very slowly given the thick leaf cuticles and the strong stomatal control in the detached leaves. Thus, it took up to 50 h to complete each P-V curve. During dehydration, weight loss was determined on an analytical balance and water potential (Ψ) measured immediately by using the pressure chamber. The water content at full turgidity was estimated for each sample according to Ladiges (1975). Then, the reciprocal of Ψ ($1/\Psi$) as a function of relative water content (RWC) was plotted. These plots were used to calculate osmotic potential at full ($\Psi_{(100)}$) and zero ($\Psi_{(0)}$) turgor, RWC at zero turgor (RWC_0) as well as apoplastic (A) water content (Turner 1981, Tyree & Hammel 1982). The volumetric elastic modulus (ε) was calculated as the slope of the relationship of turgor pressure (Ψ_p) above zero as a function of RWC.

Wood characteristics

Two branches between 1.0–1.2 m in length were sampled from the upper crown of each tagged tree early in the morning and wrapped in wet plastic bags in the field for subsequent indoor measurements. Segments of terminal twigs were subsampled from each branch. The first subsample consisted of three segments of 8–12 cm in length from each branch and was used to determine wood properties. Thus, six samples from each tagged tree were obtained. The segments were debarked, their fresh mass (W_f) was determined and their fresh volume (V_f) was obtained as the mass of displaced water. Afterwards, the segments were oven-dried at 90–95 °C until constant mass to obtain the dry mass of each segment (W_d). Stem water content (W_c) was determined as the difference between W_f and W_d for each segment, and wood density (ρ_w) was determined as W_d per unit of V_f (Siau 1984). Wood is made of water, solids and gas, with volumetric fractions of each of them termed V_w, V_s and V_g, respectively. These fractions were calculated following the relationships: $V_w = ((W_f - W_d)/(\rho_{water} V_f)) \times 100$, $V_s = (W_d/(\rho_s V_f)) \times 100$ and $V_g = 100 - V_w - V_s$, where ρ_{water} and ρ_s are the density of water and solids, respectively (Siau 1971, Whitehead & Jarvis 1981). The ρ_s was assumed to be constant at 1.53 g cm^{-3} (Siau 1971).

Hydraulic parameters

The second subsample was composed of three segments from each branch, 20–25 cm in length, and was used for all the hydraulic measurements. Length, diameter (without bark) and leaf area for each stem-sample was recorded, as required for further calculations. After, stem segments were kept wrapped in wet tissue paper and stored in plastic bags until measurements were completed, on the same day of collection. Hydraulic conductivity measurements were made by using an apparatus described elsewhere (Sperry *et al.* 1988b). In order to prevent microbial growth, the permeating liquid employed was a solution of 10 mmol KCl in pre-filtered (0.2 μm) water, as recommended by Sperry & Saliendra (1994). Hydraulic measurements were determined gravimetrically, the height of the water source was recorded for each measurement to determine the water gradient pressure and the ambient temperature was measured to determine water viscosity. The water flowing through each stem segment was collected in three pre-weighed vials that were subsequently re-weighed to estimate the water flow in 2–4 min. The mass of water that passes per unit of time (kg s^{-1}) divided by the gradient pressure (MPa m^{-1}) was expressed per stem xylem cross-sectional area to obtain specific conductivity (K_x, kg m^{-1} s^{-1} MPa^{-1}) or per distal leaf area to obtain leaf specific conductivity (K_l, kg m^{-1} s^{-1} MPa^{-1}). Once the hydraulic measurement was completed, a section of 3 cm (the third subsample) was excised from each segment and fixed in a mixture of alcohol 50%, formaldehyde and acetic acid (FAA: 18:1:1), to be used for xylem anatomy.

Xylem anatomy

Xylem anatomy was studied in transverse sections of stem segments sliced by hand, stained with toluidine blue (0.5%) and mounted permanently in glycerol. Photographs were taken by means of a camera (Model MC80, Zeiss, Germany) attached to a microscope (Model Axioskop, Zeiss, Germany). Quantitative analysis was performed on the photographic material. The area of the stem cross-section occupied by xylem tissue was determined for each sample. Huber values (H_v, m m^{-2}) were calculated as the stem cross-sectional area of xylem tissue (m^2) per leaf area (m^2). Vessel frequency and diameter of each vessel were measured for each stem. The diameter of each vessel (anatomical ratio; d_a) was calculated as the equivalent circle diameter. The variables used to characterize the twig xylem anatomy

Table 1. Midday (minimum) leaf water potential (Ψ) during rainy (RY) and rainless (RL) days, as well as pressure-volume parameters: osmotic potential at full (Ψ) and zero turgor (Ψ), relative water content at zero turgor (RWC$_o$), apoplastic water content (A) and elastic modulus (ε), measured in *Catostemma sancarlosianum* (*Cs*), *Heteropterys* sp. (*H*), *Pachira sordida* (*Ps*), *Remijia morilloi* (*Rm*) and *Retiniphyllum concolor* (*Rc*). Each value is the mean ± SE of measurements taken in three trees per species. For each parameter, means followed by the different letter were statistically different at P < 0.05.

Parameter	Species				
	Cs	*H*	*Ps*	*Rc*	*Rm*
RY Ψ (MPa)	−0.96 ± 0.08	−1.00 ± 0.06	−1.05 ± 0.07	−0.85 ± 0.15	−0.90 ± 0.08
RL Ψ (MPa)	−1.65 ± 0.04	−1.65 ± 0.08	−1.42 ± 0.06	−1.33 ± 0.07	−1.53 ± 0.07
$\Psi_{\pi(100)}$ (MPa)	−1.60 ± 0.12	−1.35 ± 0.03	−1.55 ± 0.08	−1.41 ± 0.16	−1.50 ± 0.17
$\Psi_{\pi(0)}$ (MPa)	−1.89 ± 0.05	−1.97 ± 0.07	−1.98 ± 0.06	−1.95 ± 0.18	−1.87 ± 0.22
RWC$_0$ (%)	92 ± 2a	74 ± 3d	87 ± 1ab	78 ± 2cd	84 ± 1bc
A (%)	43 ± 4a	16 ± 3b	40 ± 3a	21 ± 2b	18 ± 1b
ε (MPa)	14 ± 3a	6 ± 1b	16 ± 3a	15 ± 2a	6 ± 1b

were: vessel density (number of vessels mm^{-2}), mean conduit diameter, predicted hydraulic conductance and estimated mean hydraulic diameter. The sum of all vessel diameters to the fourth power (Σd_a^4) was used as the predicted hydraulic conductance according to the Hagen–Poisieulle Law (Choat *et al.* 2005, Sperry & Saliendra 1994). The frequency distribution by d_a class was determined for each plant group. Similarly, the contribution to water conductance of each diameter class was expressed as a percentage of the total Σd_a^4. The hydraulic diameter (d_h) was calculated by weighing each conduit to its contribution to Σd_a^4 by using the relationship ($\Sigma d_a^5/\Sigma d_a^4$; Choat *et al.* 2005, Sperry & Saliendra 1994, Sperry & Sullivan 1992).

Statistical analysis

Measurements were carried out with independent replicates taken randomly. For each parameter, the normal distribution and homogeneity of the data were determined and subsequently one-way ANOVA was used. Afterwards, statistical differences among means were determined with a posteriori LSD or Duncan test when variances were homogeneous or non-homogeneous, respectively. Significance level was set at P ≤ 0.05. Statistical analysis was performed using SPSS (SPSS 10.0 for Microsoft Windows, SPSS Inc., Chicago, USA).

RESULTS

Leaf water relations

Minimum leaf water potential (Ψ) measured under two contrasting conditions showed that during rainy days Ψ (near 1.0 MPa) was considerably higher than during rainless days (−1.33 to −1.65 MPa; Table 1). Additionally, Ψ was remarkably similar across the five species. Leaf P-V analysis showed that osmotic potential

at full ($\Psi_{\pi(100)}$) and zero turgor ($\Psi_{\pi(0)}$) was comparable among species as well. Turgor loss ($\Psi_{\pi(0)}$) occurred in all species at lower Ψ than the minimum values recorded in the field (Table 1). Examples of the Höfler diagrams derived from P-V curves characterized the responses of water relation parameters to RWC for two contrasting species: *Heteropterys* sp. and *P. sordida* (Figure 1). Variation in relative water content at zero turgor (RWC$_o$), apoplastic water (A) and volumetric elastic modulus (ε) accounted for major differences in leaf tissue water relations across species (Table 1, Figure 1). Thus, *Heteropterys* sp. and *R. concolor* lost turgor at lowest RWC$_o$, and had the lowest A content and more elastic cells (<ε). By contrast, *C. sancarlosianum* and *P. sordida*, with less elastic cell walls (>ε), had relatively high RWC$_o$ and a shifting of symplastic water volume to the apoplast, whereas, *R. morilloi* had an intermediate behaviour with inelastic cell walls like *C. sancarlosianum* and *P. sordida*, but with A content comparable to *Heteropterys* sp. and *R. concolor*, resulting in an intermediated RWC$_o$. Thus, increasing tissue elasticity can be regarded as a mechanism of turgor maintenance in response to leaf dehydration. This suggested that *Heteropterys* sp. and *R. concolor* might have a greater potential for acclimation to leaf dehydration and maintenance of high water potentials. Leaves of *C. sancarlosianum*, *P. sordida* and *R. morilloi* with rigid cell walls could undergo a lower water potential for small changes of water volume.

Wood characteristics

Wood and xylem characteristics of terminal branches are shown in Table 2. The species showed some significant differences in their wood water content (W$_c$) as well as in density (ρ_w); *C. sancarlosianum* had the lowest W$_c$ and the highest ρ_w and the reverse trend was found in *R morilloi*. Thus, wood water content and density were negatively associated (r = 0.96; P < 0.005). As expected, the volumetric fraction of water (V$_w$) and the solids (V$_s$)
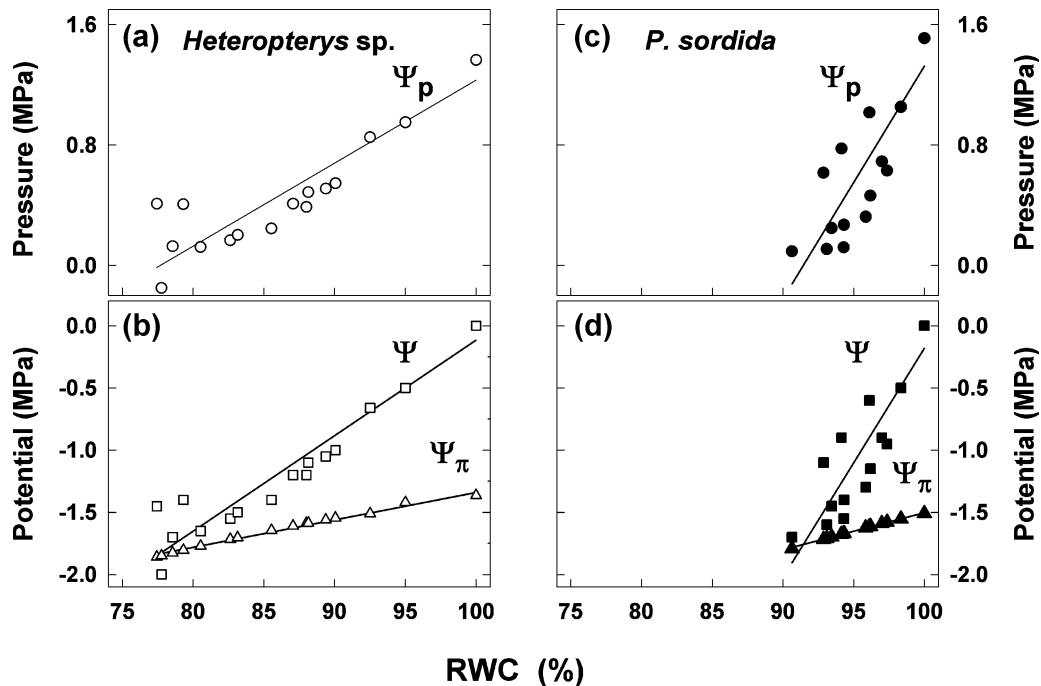
Figure 1. Höfler diagrams showing water potential (Ψ) and components: osmotic potential (Ψ_π) and turgor pressure (Ψ_p) as a function of relative water content (RWC) in two species with contrasting leaf tissue water relations: *Heteropterys* sp. (a, b) and *Pachira sordida* (c, d). Plots were derived from four P-V curves for each species. Linear regressions are shown and equations are: $\Psi_p = 0.055\,RWC - 4.27$ ($r = 0.93$; $P < 0.0001$), $\Psi_\pi = 0.021\,RWC - 3.54$ ($r = 0.99$; $P < 0.0001$), $\Psi = 0.076\,RWC - 7.79$ ($r = 0.96$; $P < 0.0001$) for *Heteropterys* sp. and $\Psi_p = 0.154\,RWC - 14.14$ ($r = 0.87$; $P < 0.0001$), $\Psi_\pi = 0.029\,RWC - 4.47$ ($r = 0.90$; $P < 0.0001$), $\Psi = 0.184\,RWC - 18.61$ ($r = 0.90$; $P < 0.0001$) for *Pachira sordida*.

followed the same trend as W_c and ρ_s, respectively. The gas fraction (V_g) was comparable across species and ranged between 8–13%, differences between species not being statistically significant (Table 2).

Xylem characteristics

There were significant differences among species in both the fraction of the transverse section occupied by the xylem and in vessel density (Table 2). Vessel anatomical diameter (d_a) varied across species, and *R. morilloi* (widest vessels) had vessels 47% wider than those in *Heropterys* sp. (narrowest vessels; Table 2). Hydraulic diameter (d_h) varied across species as well, but the maximum difference across species declined to 33% (*R. morilloi* vs *C. sancarlosianun*; Table 2). Vessel density and shift in the diameter frequency were accounted for by interspecific differences in xylem anatomy (Table 2, Figure 2). In *C. sancarlosianum* and *R. concolor*, vessels larger than 70 and 80 μm, respectively, were absent. A balanced distribution of vessel diameter between 10–50 μm was found in *R.*

Table 2. Water content (W_c), wood density (ρ_w), wood volumetric fraction of water (V_w), solids (V_s) and gas (V_g), per cent of transverse section occupied by xylem tissue (Xyl), vessel density (VD, no. mm^{-2}) and anatomical (D_a) and hydraulic ratios (D_h) measured in *Catostemma sancarlosianum* (Cs), *Heteropterys* sp. (H), *Pachira sordida* (Ps), *Remija morilloi* (Rm) and *Retiniphyllum concolor* (Rc). Each value is the mean $\pm$ SE of measurements taken in three trees per species. For each parameter, means followed by the different letter were statistically different at $P < 0.05$.

| Parameter	Species				
	Cs	*H*	*Ps*	*Rc*	*Rm*
W_c (g g^{-1})	0.39 ± 0.01b	0.44 ± 0.01ab	0.44 ± 0.02ab	0.45 ± 0.01a	0.50 ± 0.04a
ρ_w (g cm^3)	0.67 ± 0.02a	0.61 ± 0.02ab	0.63 ± 0.04ab	0.61 ± 0.02ab	0.55 ± 0.95b
V_w (%)	42.9 ± 1.4b	48.5 ± 1.4ab	51.1 ± 3.1ab	51.4 ± 1.6ab	54.2 ± 4.3ab
V_s (%)	43.7 ± 1.2a	39.8 ± 10ab	41.2 ± 2.9ab	40.0 ± 1.1ab	36.1 ± 3.1b
V_g (%)	13.3 ± 2.1	11.7 ± 1.5	7.7 ± 3.8	8.6 ± 1.4	9.7 ± 1.3
Xyl (%)	64.4 ± 2.9c	78.6 ± 1.1b	59.3 ± 2.3c	85.6 ± 2.4a	74.5 ± 4.8ab
VD	314 ± 24a	124 ± 7d	252 ± 24b	155 ± 7cd	204 ± 20bc
D_a (μm)	32.8 ± 1.8bc	28.9 ± 1.3c	33.0 ± 2.7bc	36.7 ± 1.8ab	42.5 ± 4.3a
D_h (μm)	42.4 ± 2.3b	52.0 ± 3.1ab	52.7 ± 4.2ab	47.7 ± 3.3ab	56.3 ± 4.96a
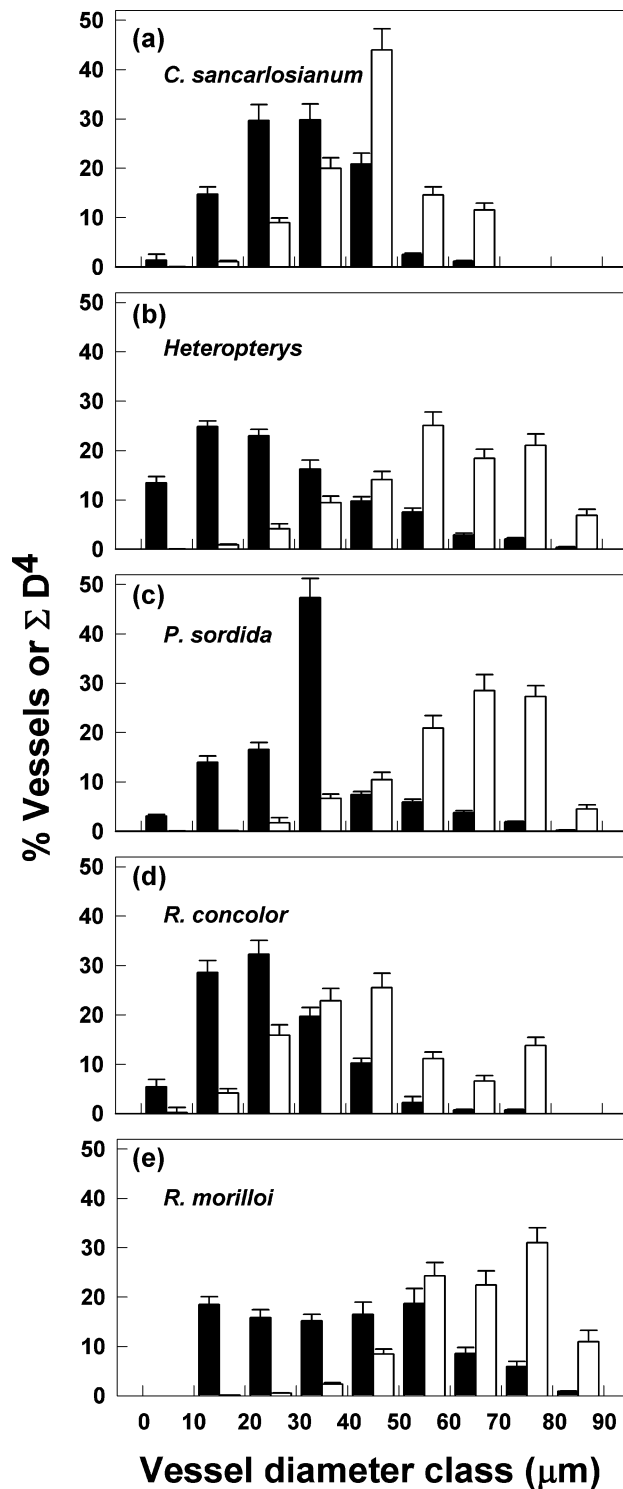
Figure 2. Vessel diameter class in the stems of *Catostemma sancarlosianun* (a), *Heteropterys* sp. (b), *Pachira sordida* (c), *Retiniphyllum concolor* (d) and *Remijia morilloi* (e). Black bars represent percentages based on total vessel number and white bars are the conductance percentage based on the sum of all vessel diameters to the fourth power (Σd_a^4). This reflects the relative hydraulic importance of each diameter class as estimated by the Hagen–Poiseuille Law. The bars are the means of measurements taken in three trees per species and SE.

morilloi. However, the predicted hydraulic conductivity ($\Sigma\ d_a^4$) per diameter class also shifted towards wide vessels in all species (Figure 2). This means that all species depended on fewer wide vessels for water transport.

Hydraulic characteristics

Stem hydraulic properties varied according to changes in the xylem structure. Thus, Huber value was slightly higher in *R. concolor*, but differences among species were not statistically significant (Figure 3a). Both hydraulic conductivity per xylem area (K_x) and per leaf area (K_l) tended to increase with vessel density (Figure 3b, c). Thus, positive and statistically significant relationships between K_x and vessel density ($r = 0.97$; $P < 0.006$), and between K_l and vessel density ($r = 0.95$; $P < 0.011$) were found. *Catostemma sancarlosianum* had the highest K_x and K_l with the highest leaf density as well (Table 2). Thus, K_l of *R. concolor*, *R. morilloi* and *P. sordida* were comparable, and the lowest value was found in *Heropterys* sp.

DISCUSSION

In this study, the first comparison of xylem structure, hydraulic characteristics and leaf tissue water relations of sclerophyllous species coexisting in the bana vegetation is presented. Minimum Ψ was observed on rainless days, which averaged -1.53 ± 0.61 MPa, a value significantly lower than that of -0.94 ± 0.10 MPa found during rainy days. These averaged Ψ values and their trend agreed entirely with previous studies where frequency of drought spells was assessed monthly in conjunction with measurements of leaf Ψ and stomatal conductance in these species during 1976–1977 (Sobrado 1977). Drought periods can last from 3–8 d in this area at any time of the year, and between one to four times per year they last 15–20 d, particularly during February–March and October–November (Medina *et al.* 1978, Sobrado & Medina 1980). Sandy soils occupied by this sclerophyllous vegetation have low water-retention capability and the water table can drop below the main root zone during drought spells, or become waterlogged for a few hours after rain (Bongers *et al.* 1985). The average Ψ_π between full and zero turgor was -1.48 ± 0.05 and -1.92 ± 0.05 MPa, respectively, across species. This means that, on average, if the leaf Ψ falls below -1.92 ± 0.05 MPa, the leaf turgor is lost. Lower Ψ_π can enhance the plant-soil water potential gradient, thereby favouring water uptake above water loss. However, the species maintained the minimum Ψ within a safety range above the critical value for turgor loss, of about 0.97 ± 0.11 and 0.41 ± 0.12 MPa during rainy and rainless days, respectively. This safety range
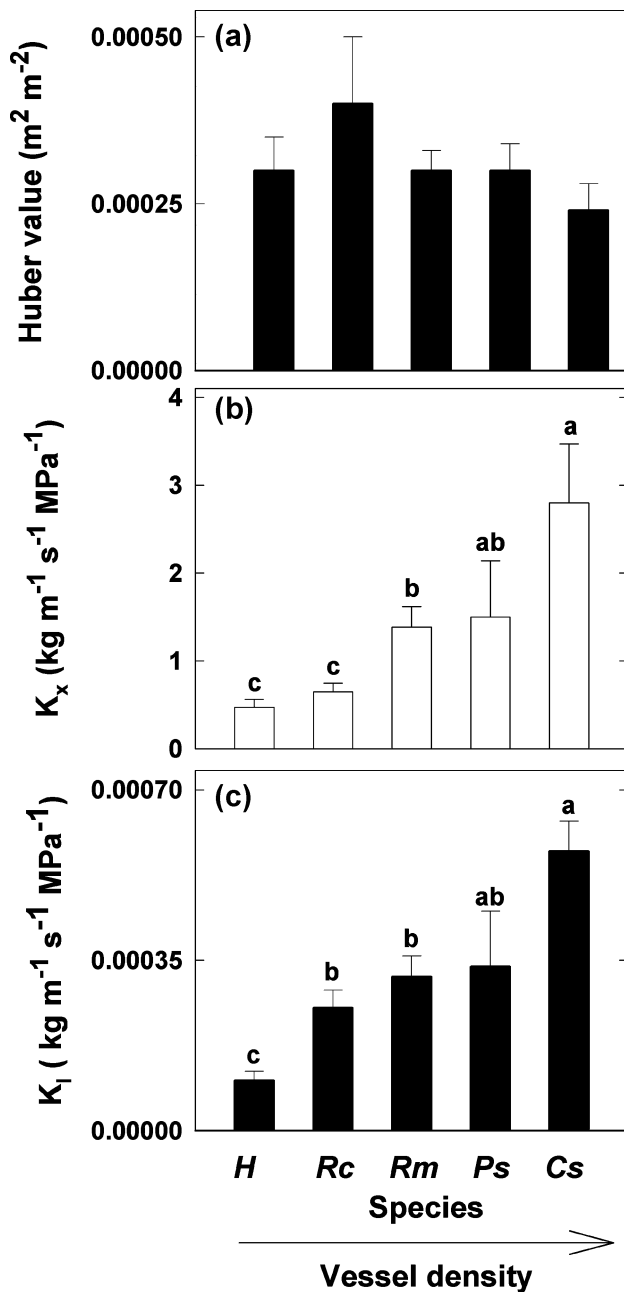
Figure 3. Huber value, xylem specific conductivity (K_x) and leaf specific conductivity (K_l) in the stems of *Catostemma sancarlosianun* (*Cs*), *Heteropterys* sp. (*H*), *Pachira sordida* (*Ps*), *Remijia morilloi* (*Rm*) and *Retiniphyllum concolor* (*Rc*). Species are arranged as vessel density increases. The bars are means of measurements taken in three trees per species and SE. Different letters indicate significant differences (P < 0.05).

may be important for xylem integrity. Previously, we have occasionally recorded Ψ of about -1.8 MPa (Sobrado 1977). Thus, we cannot preclude that in unusually long dry spells, these species can reach low Ψ and perhaps lethal levels of embolisms in terminal branches. Occasionally, damaged leaves had been observed in the

field. The range of Ψ_π values in these species was much higher than those found in sclerophyllous species from tropical seasonal dry forests with several rainless months (< 3.0 MPA; Olivares & Medina 1992, Sobrado 1986). However, our Ψ_π values compare well to those found in Mediterranean sclerophyllous leaves which are not particularly drought resistant (Kyriakopoulus & Richter 1991, Salleo & Lo Gullo 1990, Salleo *et al.* 1997). The anatomical structure typical of sclerophyllous leaves seems to appear first in humid areas and later migrate to more arid zones (Salleo *et al.* 1997). The species differed in their leaf elasticity: 5.8 ± 0.5 MPa in *Heteropterys* sp. and *R. concolor*, compared with 14.1 ± 1.2 MPa in *C. sancarlosianum*, *P. sordida* and *R. morilloi*. Leaf blades with lower elasticity are composed of smaller cells with thicker cell walls (Cutler *et al.* 1977). An increase in ε as a consequence of changes in leaf structure has been considered the most significant leaf-level adaptation to water limitations on a global scale, considering that intracellular solute concentration is limited (Niinemets 2001). The dominant species *C. sancarlosianum*, *P. sordida* and *R. morilloi* had the least elastic ($>\varepsilon$) leaf tissue. Low ε allows leaf dehydration to reach lower levels, while still maintaining their Ψ within the range of positive turgor, which may be beneficial during drought as well. Thus, both high and low ε have beneficial effects for drought tolerance (Abrams 1990, Bowman & Roberts 1985, Roberts *et al.* 1980). Summarizing, the five species experience comparable midday water potential, similar Ψ for turgor loss, maintenance of a safety range of Ψ above turgor loss and capability to develop leaf-to-soil water potential differences for water uptake.

Wood consisted mostly of water, which averaged 0.47 ± 0.01 g g^{-1} and $49.6\% \pm 1.1\%$ for W_c and V_w, respectively. V_g was the lowest fraction and averaged $10.2\% \pm 0.8\%$ among species. Tropical woods contain lower amounts of gas compared with temperate softwoods and hardwoods (Gartner *et al.* 2004, Poorter 2008). Increase in V_g results in higher biomechanical stability, which would be advantageous for tall trees receiving large wind force loads which increase surface stress (Gartner *et al.* 2004). The ρ_w and V_s have been regarded as measures of mechanical support and higher values correspond to species with slower growth (Lawton 1984).

Comparison of xylem density across Amazonian habitats has shown a very wide range from 0.24 up to 1.13 g cm^{-3} reflecting the contrasting climatic conditions found in the whole basin (Patiño *et al.* 2008). In this study, ρ_w and V_s averaged among species 0.61 ± 0.02 g cm^{-3} and $40.2\% \pm 0.7\%$, respectively. Across tropical species, wood with low ρ_w is cheap to construct and allows fast growth, whereas high ρ_w results in persistent wood and increases survival (Poorter 2008, Poorter & Bongers 2006). Furthermore, ρ_w and leaf mass per unit leaf area have been closely correlated suggesting that

both parameters are related with growth capability and life span (Poorter & Bongers 2006). Studied species have leaves with a high leaf mass to leaf area ratio, which would require stems with enough biomechanical strength to resist bending stress with minimum deflection. In addition, a clear relationship between ρ_w of tropical species and the amplitude of daily changes in leaf Ψ has been established (Meinzer 2003). In concordance with this relationship, the studied species would undergo diurnal changes in Ψ near to 1.1 MPa, which is consistent with the recorded range (Sobrado 1977). In temperate plant species, ρ_w has been positively correlated with the threshold xylem water potential for 50% loss of hydraulic conductivity as well (Hacke & Sperry 2001). However, it remains to be established if such a relation holds for tropical species.

The average d_a of 34.7 $\pm$ 1.2 μm in our twigs samples was low compared with values from 65–250 μm found in main stem wood from another Amazonian sandy-soil forest (Woodcock et al. 2000). However, vessel density was higher in this study (120–320 vessels mm^{-2}) than was reported in that study (4–80 vessels mm^{-2}). Anatomical differences in xylem tissue would result in different hydraulic capacities and transpiration rates (Schultz & Matthews 1993, Tyree & Ewers 1991, Tyree & Zimmermann 2002). Vessels with large diameter and pore size in inter-vessel pit membranes are evolutionarily favoured for efficient water conduction (Tyree et al. 1994). Thus, the d_h average was 49.9 $\pm$1.7 μm across species and between 16% and 90% of the water transport would occur in vessels wider than 50 μm, but the amount of vessels in this range was only between 4% and 33%. This indicated that more frequent narrow vessels would not compensate for less frequent larger vessels in terms of potential for water flow. The fact that these species depend on the small number of large vessels for most of their water transport capability suggested that their xylem is highly vulnerable to cavitation. Thus, the large vessels allow low investment in xylem structure in order to obtain high permeability. Water conductance efficiency, provided by wider vessels, would be advantageous for this species because leaves were unable to develop very negative water potentials in order to maintain water loss. However, high transpiration rates seem to be restricted to a few hours daily (Sobrado 1977), so as to prevent xylem cavitation. Despite the fact that more numerous smaller vessels could act as an auxiliary transport network to maintain some water flow if the larger vessels became embolised, preservation of those fewer and wider elements may have paramount importance to maintain a high leaf water supply. Xylem anatomy and hydraulic parameters indicated that both traits are structurally and functionally coordinated in this study. Thus, species with low vessel density had the lowest K_x and K_l as well, which suggested that larger pressure gradients would be required to maintain high transpiration rates. Across species, lack of correlation of K_x and K_l with vessel diameter might suggest that vessel diameter might not correlate well with cavitation resistance across species (Choat et al. 2008). The K_x is a measure of transport efficiency per unit of xylem area (Zotz et al. 1998), whereas leaf specific conductivity (K_l) is a useful measurement of hydraulic sufficiency of stems in supplying water to the leaves (Tyree et al. 1994). Therefore, water transport through xylem was less efficient in Heteropterys sp. and R. concolor. Specifically, it shows that species with lower capability for xylem water transport have leaves with more elastic leaf tissue. Thus, these species can undergo larger dehydration of leaf cells and still maintain turgor and turgor-related processes. Across species K_x and K_l averaged 1.4 $\pm$ 0.22 and 0.00033 $\pm$ 0.000045 kg m^{-1} s^{-1} MPa^{-1}, respectively. These values were of a similar order of magnitude as reported for other tropical species (Sperry 2003, Tyree & Zimmermann 2002, Zotz et al. 1998).

CONCLUSIONS

Despite the fact that the leaves of the bana species are stiff, strong and tough, they are unable to sustain large water-potential drops (< -1.9 MPa). All species depend on relatively less abundant larger vessels for water transport, and leaf water supply is favoured in species with higher vessel density, which have a larger number of wider vessels as well. Midday regulation of water loss by stomatal closure may be an effective mechanism to preserve xylem integrity of these species. Thus, the minimum Ψ was conservative and well below the critical value for leaf turgor loss. When transpiration is severely reduced at midday, vertically oriented leaves help prevent overheating damage (Medina et al. 1978, Sobrado 1977). Despite this, at midday leaf blades absorb more photons than can be used in carbon assimilation, and photosynthetic apparatus undergoes down-regulation due to non-chronic photo-inhibition (Sobrado 2008). Consequently, these species should maximize production in the short-term with high water transport and very low water-use efficiency, and become highly conservative at times of maximal irradiance. This would result in very high costs due to high leaf blade construction and maintenance costs with reduced photosynthetic capacity (Sobrado 2009). A reduced daily carbon gain and productivity would further limit these species as effective competitors.

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