

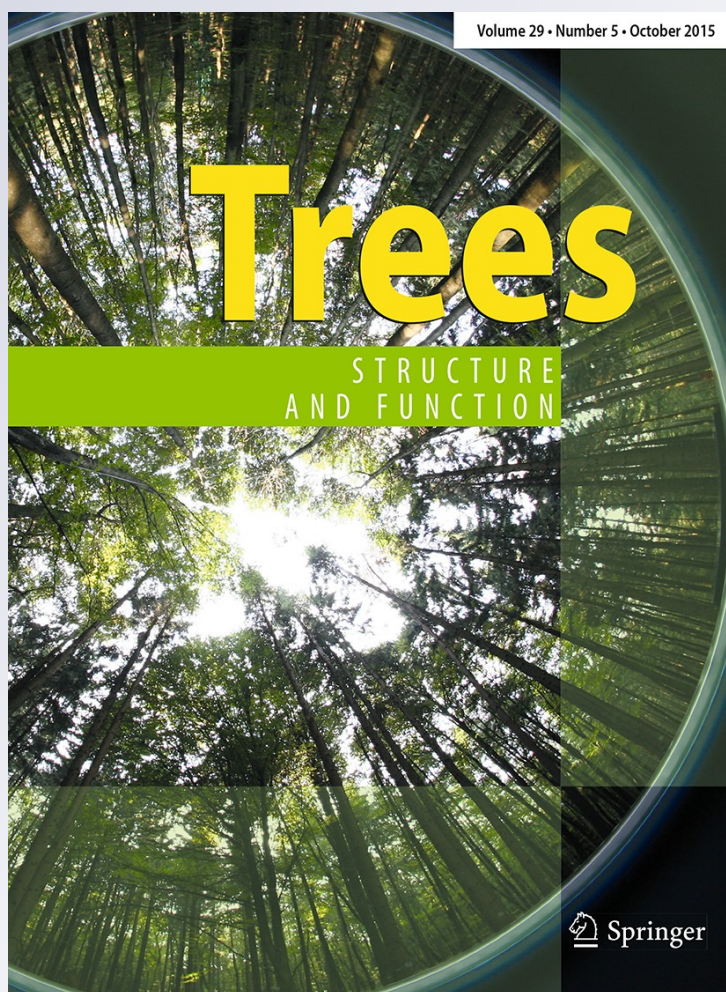
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Ecological applications of differences in the hydraulic efficiency of palms and broad-leaved trees

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Abstract

Key message In tropical forests, co-occurring woody monocot and dicot species adapted different water use strategies highly depending on their investment in the hydraulic conduit properties.

Abstract We studied the hydraulic efficiency of palms and broad-leaved tropical tree species from a moist tropical lowland forest in the Central Brazilian Amazon. Therefore, we harvested 34 trees and 10 açai palms and measured vessel size and frequency at diameter at breast height and additionally at the base of the crown shaft for the palms. Further, we assessed the active xylem area to estimate the hydraulic conductivity through Hagen Poiseuille's adapted theoretical equation. Mean vessel diameter in dicot trees was $127.62 \pm 49.22 \mu\text{m}$ with an average 9.09 ± 6.50 vessels per mm^2 . Mean conduits sizes at the base ($h = 0.10 \text{ m}$) of palm trees were larger with $288.20 \pm 32.96 \mu\text{m}$ and less frequent with 1.40 ± 0.46 vessels per mm^2 . Hydraulic conductivity was on average $3.31 \pm 4.59 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ for dicot trees. Mean hydraulic conductivity in açai palms was $20.45 \pm 10.6 \text{ kg m}^{-1} \text{ s}^{-1}$

MPa^{-1} at the base, and increased to $124.73 \pm 55.2 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ at the crown base. Hydraulic conductivity at the base of the crown was higher than in the base of the trunk due to the high density of vessels in a small cross-section in this height. Furthermore, we found a species-independent relationship between vessel diameter and frequency. We conclude that the differences found in the hydraulic efficiency give some evidence that palms have a lower occurrence of embolism and cavitation than trees, which is due to stiffer and stronger conduit pathways and efficient drought-avoiding strategies. The differences in hydraulic architecture between palms and trees imply different water use patterns thus varying niche differentiation, but this does not consequently need to be an excluding factor for coexistence in the same environment.

Keywords Wood anatomy · Plant functional groups · Ecohydrology · Monocot · Dicot · Terra firme · Vessel size

Introduction

The Brazilian Amazon is recognized by its hyper-diverse flora, but the functional diversity of species has only recently been studied more profoundly. Despite the high tree diversity in the Amazon, Steege et al. (2013) and Pitman et al. (2001) suggest that only 1.5 % of the species pool of the woody plant species set half of the trees in the Amazon. This hyperdominance is characterized by habitat specialist covering a large geographical range. Interestingly, the three most abundant species in the Amazon are represented by three distinct functionally different species. The most abundant woody species is the monocot species *Euterpe precatoria* (~2 %) that belongs to the Palmae family,

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followed by two dicotyledonous tree species from the genera *Protium* and *Eschweillera* (Steege et al. 2013).

Dicot and monocot plants are characterized by distinct different growth pattern as well as functional and ecological different traits. One of the main differences is in their hydraulic architecture. Perennial woody dicotyledonous species possess a vascular tissue in a continuous ring beneath the bark that grows on an annual basis that allows an increase in stem diameter or wood production (Perry 1991). Perennial woody monocotyledonous species, like palm trees, have a fixed number of vascular bundles (phloem and xylem cluster) which increase in diameter through a sustained primary growth (expansion of parenchyma cells and intercellular space) (Perry 1991; Renninger et al. 2013; Tomlinson 1979; Waterhouse and Quinn 1978; Zimmermann 1983). After maximal apical diameter expansion and start of height growth, palm stems expand little or nothing in diameter. (Perry 1991). This growth pattern and vascular system differences affect their size, biomass production and, consequently, water use properties; especially due to palm trees' permanent number of conduits that need to function effectively throughout the plant's lifespan growth and development (Renninger et al. 2013; Waterhouse and Quinn 1978; Tomlinson 1979). These factors can be the reason why these distinct functional groups coexist in the same biome but sometimes are located in a specific stand location (Kunert et al. 2013). The Amazon forest is a biome composed of different environments which correspond to different plant species composition and ecological traits that can be due to topographic variation, hydraulic efficiency and water use rates of these different species (Vormisto et al. 2004; Kunert et al. 2013; Wagner et al. 2012).

Hydraulic efficiency is defined as the hydraulic conductance per fixed vascular volume (Sperry et al. 2008). According to Murray's law, the most efficient vascular arrangement appears to be single branched ducts that taper from wider diameters at the base and narrowing up at the top (Murray 1926). This parameter can be evaluated through hydraulic conductivity (Ks), which is the conductance (volume flow rate per pressure drop) per unit length divided by sapwood cross-section that is a measure of the plant's porosity (Tyree et al. 1991; Tyree and Zimmermann 1983; Sperry et al. 2008). Since this variable considers the physical properties of water, vessel dimensions and active xylem area, it results in a value that expresses how easily or difficult water is being transported through the conduits (Sperry et al. 2008). Therefore, conductivity will be directly related to the plant's ecological trait and growth pattern. Dicot trees use their assimilated carbon to produce wood periodically (height and diameter/vessels), leaf biomass, new branches and roots, but are highly vulnerable to embolism and cavitation (Sperry et al. 2008; Meinzer et al. 2010; Hacke et al. 2006). Monocot palm trees have long and

fibrous fronds that require a large amount of carbon and water to be built and maintained, but palms do not develop branches, deep roots and are little affected by embolism at the trunk (Tyree and Ewers 1991). Palms clearly differentiate mechanically and hydraulically in different regions of the stem (the portion closer to the bark is extremely rigid providing mechanical stability and the central portion of the cross-section with large vessels for hydraulic uplift). In dicot trees, a given cross-section of wood tissue serves both functions (Sperry 1986; Zimmermann 1983; Rich 1987). Therefore, palms are considered to be hydraulically more efficient than trees (Renninger et al. 2013).

Although palm trees are considered to have a higher hydraulic efficiency than trees, they use on average more water than a similar sized tree and that might cause water limitations during certain times of the year (Kunert et al. 2013; Renninger et al. 2013). Due to their higher water use, palm trees are getting probably outcompeted by dicot trees in well-drained upland plateau areas in the Amazonian lowland forest (Kunert et al. 2013). Thus, palm trees are restricted, but not limited, to seasonally flooded valleys (denominated locally as "baixios") and riparian areas, (Kunert et al. 2013; McClain et al. 1997). These flooded valleys, along with well-drained upland plateaus, are embedded in a widespread forest type in the Central Amazon called "terra firme", which is not affected by seasonal inundations (McClain et al. 1997). Palm trees form almost monospecific and very uniform communities in these seasonally flooded valleys, but can also be rarely found growing among predominant dicot trees in well-drained plateaus area (McClain et al. 1997; Porto et al. 1976; Ruiz and Alencar 2004; Henderson et al. 1995; Ribeiro et al. 1999).

Plant competition, vascular differences and habitat restrictions between these two functional groups are intriguing. For better understanding in how dicot and monocot species coexist in tropical environments, we hypothesized that differences in plant hydraulics are the main reasons for the two plant groups to occupy a certain habitat. To confirm this hypothesis, tree and palm hydraulic conductivity were estimated and related to growth and wood anatomy variables. Furthermore, we wanted to reveal if palm trees have a significant variation of hydraulic conductivity at different heights, since palms are not characterized by secondary growth and the development of branches.

Materials and methods

Study site and sample trees

The present study was conducted in an Amazonian old growth forest lowland forest located approximately 70 km northeast from the city of Manaus, Brazil (02°37'31.8"S;

60°08'24.7"W). The study site is part of Experimental Station for Tropical Silviculture ZF-2 of the Brazilian National Institute for Research in the Amazon (INPA). The area selected for the experiment is located 18 km along the vicinal road of ZF-2.

The terrain surrounding the experimental station has an undulating topography that is classified as “baixio” in the lowest portion (valleys) and “plateau” at the flat terrain and highest portion, which is covered with a species-rich “terra firme” forest. The study area is comprised inside a large plateau area and is characterized by elevated temperatures and high humidity throughout the whole year. Average annual temperature is 25.8 °C and relative humidity between 84 and 90 % throughout the year (Oliveira and Amaral 2004; Mota and Medeiros 2002). Annual accumulated precipitation is on average 2547 mm, with on average only one dry month in September but with longer dry spells between June and October in exceptional dry years (Mota and Medeiros 2002). Vegetation on plateaus is predominantly evergreen and contains a high variety of tree species. The periodically flooded valleys (“baixios”) present a lower diversity composed predominantly by palm trees (Bravard and Righi 1989; Castilho et al. 2006; da Silva et al. 2015).

Thirty four sample trees were selected randomly in a period between December 2012 and May 2013, which corresponds to the region's rainy season. There was no predetermined tree species or group. Therefore, from those 34 sample trees were 27 distinct tree species identified through wood anatomy characteristics and, if necessary, botanical samples. Selection was based on logistics and tree size criteria. Diameter at breast height (DBH) varied between 5 and 40 cm and trees were located close to the vicinal road and about 100 m inside the forest. Tree individuals were not over 40 cm at DBH due to logistics and laboratory handling difficulties. Logs were extracted at breast height ($h = 1.30$ m) for sapwood area determination and wood samples for anatomical analyses.

Palm tree sampling and study site

Palm tree sampling was conducted in a periodically inundated valley (“baixio”) near the ZF-2 vicinal road and 8 km from the tree study area, but still inside the same Experimental Station-ZF-2 (INPA) (da Silva et al. 2015). The chosen palm tree species was *Euterpe precatoria* Mart. (Arecaceae) and ten individuals with DBH >10 cm and between 7 and 20 m in height were harvested during February and March, 2013, which is embedded in the region's rainy season. These individuals had logs extracted at base height ($h = 0.10$ m) and at the base of the live crown (height of sectioning varied between individuals) for sapwood area determination and wood samples for the

anatomical analyses. Only one species was chosen due to literature evidence that palm trees do not have significant variations between palm species on their stem conductive area and vascular anatomy (Rüggeberg et al. 2008; Rich 1987). This species was chosen due to its economic importance and considered as a hyperdominant palm species in the Brazilian amazon lowlands (“baixios”) (Steege et al. 2013), which facilitated its location and harvesting. Commonly known as “açai palm”, *Euterpe precatoria* is a native species that grows in the amazon forest in periodically flooded areas (Kunert et al. 2013). This species grows solitarily with stem diameters ranging between 5 and 23 cm and reaches around 20 m in height (Lorenzi et al. 2006; Henderson et al. 1995).

Hydraulic conductivity

Water flow is given through Hagen–Poiseuille's theoretical capillary conductance equation by calculating the sum of vessel diameters elevated to the fourth power (Mulkey et al. 1996). Therefore, vessel diameter is highly correlated to dicot and monocot trees hydraulic conductance (Ewers and Fisher 1989). This high correlation resulted in Tyree and Zimmermann (1983) specific hydraulic conductivity equation (K_s). We used this specific equation to estimate the hydraulic conductivity out of the metaxylem vessel diameters. The equation by Tyree and Zimmermann (1983) is as follows:

$$K_s = \frac{\pi/8 \times \eta(\sum r^4)}{A_s} \times \rho \text{ [kgm}^{-1}\text{s}^{-1}\text{MPa}^{-1}\text{]}$$

In which ρ is water density (equivalent to 998.2 kg m⁻³ at 20 °C), r is xylem vessel radius (m), η is water viscosity (equivalent to 1.002×10^{-3} MPa at 20 °C) and A_s is sapwood area. The maximum of the hydraulic conductance for a given sap wood area was used to determine the hydraulic efficiency of monocot and dicot trees (Renninger et al. 2013).

Sapwood area determination

The method chosen for sapwood area delimitation was through immersion of tree and palm tree logs in dye solution (Reyes-Acosta et al. 2012; Umebayashi et al. 2007; Kitin et al. 2010). The dye used was indigo carmine, which has as an advantage over other type of dyes since it is not absorbed by living cells, which can stain areas that are not equivalent to conductive sapwood area (Davies et al. 2007; Sano et al. 2005). The logs taken from trees and palms were taken immediately after harvesting to a container filled with indigo carmine solution. Logs were left immersed for hours or days until blue staining was fully apparent on the top cross-section surface indicating the active conductive area.

Tree diameter was obtained through the average between two measurements in the individual's disc (wider diameter and narrower diameter). Sapwood area (A_s) was measured using five radii marked along the cross-section starting from the pith (Barusso 1977). Each radius had two measurements: total radius [distance from the pith to the bark base (R)] and heartwood (or inactive area) radius [distance from the pith to the base of the colored area (r)]. Through each radius, we estimated total cross-section area and heartwood cross-section area, that when subtracted resulted in the conductive sapwood area of that tree individual [$A_s = \pi(\bar{R}^2 - \bar{r}^2)$]. Including five different radii measurements guarantees that variations in irregularly shaped cross-sections were assessed (e.g., sapwood area with flawed staining areas).

Wood anatomy

Dicot and monocot tree samples were characterized through macroscopic description (wood characteristics for species identification) and microscopic description techniques (histological slides and maceration for vessel diameter and frequency measurements). Macroscopic description followed technical standards recommended by the Pan-American Technical Standards Commission (COPANT 1974). Wood samples with dimensions $1.5 \times 2.0 \times 3.0$ cm were taken from each tree and palm log sections and were characterized through specific wood structures and characteristics (heartwood color; smell; texture; type of bark; parenchyma description; and others) to determine and verify tree species (Freitas and Vasconcellos 2010). Wood samples were registered and stored at Xylotheque of the Brazilian National Institute of Amazonian Research (INPA) in Manaus, Brazil.

Histological microscope slides were made so that vessel cross-sections were apparent for diameter (μm) and frequency (mm^{-2}) measurements and tyloses occurrence. These slides were made with $18 \mu\text{m}$ histological woodcuts (from an American Optical 860 microtome) dehydrated in an ethyl series (50, 70, and 100 %) (Johansen 1940), and later dyed with safranin–fuchsin for distinct tissue cell observations. Measurements were made using an Olympus Tokyo projector at $100\times$ (TandD VR-71, T&D Corporation, Shimadachi Matsumoto City, Japan) choosing randomly 25 vessels per tree sample. Due to the fibrous palm tissues, their histological cuts were not viable for measurements. Therefore, palm wood conductive elements were dissociated from woody tissues (fibers and parenchyma) through chemical maceration developed by Johansen (1940). Small wood samples were submerged and kept 2 days in a maceration solution constituted of acetic acid, hydrogen peroxide and distilled water. When loosened and dissociated, the material was also submitted to

safranin–fuchsin dye for an accurate conductive element observations. Finally, these conductive elements were set on microscope slides and were measured also using Olympus Tokyo projector at $100\times$ (TandD VR-71, T&D Corporation, Shimadachi Matsumoto City, Japan).

Statistical analysis

Both trees and palm trees datasets were submitted to ANOVA, Pearson's correlation coefficient (r) and regressions using standard linear model ($Y = a + bX$, in which Y is hydraulic conductivity; a is line intercept; b is slope angle; and X is a biometrical variable (diameter, height, sapwood area, vessel diameter or vessel frequency) and non-linear power model ($Y = aX^b$, in which Y is hydraulic conductivity, a is normalization constant, X is a biometrical variable and b is an allometrical scale exponent) (Meinzer et al. 2005; Wullschleger and Norby 2001; Gebauer et al. 2008). These fittings were focused on determining also R^2 , S_{yx} %, F value and p value. Model fitting was executed to determine variable relationship. Statistical analyses were performed with R version 2.6.2 software (R Core Team 2013).

Results

Base and crown conductivity variation in palms

Açaí palms ranged from 11.7 to 16.6 cm in DBH and height between 7.4 and 19.6 m. The difference between base diameter and crown were nearly 50 % (Table 1). Sapwood area ranged between 54.7 and 155.5 cm^2 at base height and 3.77 and 15.62 cm^2 at crown height. Vessel diameter varied between 247.5 and 353.8 μm and frequency around 1–2 vessels per mm^2 at base height. At crown height, variation was between 177.7 and 319.5 μm and 2–4 vessels per mm^2 , respectively. Although crown vessel diameters were slightly smaller than at base height, according to COPANT 1974 standards, they are both considered as large sized conduits ($\bar{x}_{\text{Base}} = 289 \mu\text{m}$; $\bar{x}_{\text{Crown}} = 233 \mu\text{m}$). But vessel frequency at crown height was almost double when compared to base measurements. Hydraulic conductivity at the base varied between 9.64 and 46.99 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ and at crown level between 27.47 and 191.81 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$. The highest values corresponded to the individual with the largest vessel diameter, independent of sapwood area size.

Considering that the sapwood area measured in this study is equivalent to the hydroactive portion of the xylem, we hypothesized that hydraulic conductivity would be proportional to it. However, the relationship between sapwood area and K_s was not as high as expected. For

Table 1 Size, anatomical details and hydraulic conductivity for sampled açai palms

Palm (<i>N</i> = 10)	Total height (m)	Base measurements					Crown measurements				
		Base diameter (cm)	Sapwood area (cm ²)	Vessel diameter (μm)	Vessel frequency (μm)	Ks	Crown base diameter (cm)	Sapwood area (cm ²)	Vessel diameter (μm)	Vessel frequency (μm)	Ks
1	19.6	12.8	95.50	353.8	1.5	46.99	8.5	5.75	254.0	2	187.86
4	16	15.5	155.50	310.8	2	17.80	8.3	15.62	319.5	2.5	191.81
5	8	14	97.90	304.0	1	24.45	6.2	6.41	241.2	3	144.42
7	9.4	12.8	83.90	302.2	2	18.67	5	3.77	187.9	2.8	92.30
11	14.5	16.6	137.10	286.0	1	12.68	7.2	7.53	241.4	4	142.92
12	16.4	12.8	89.60	285.0	1	18.93	8.5	10.25	177.7	3.2	27.47
13	11.8	11.7	54.70	247.5	1.5	23.32	7.1	6.18	245.0	3	158.73
14	7.4	15.1	116.90	253.2	1	10.51	7.7	8.96	211.7	2.2	67.37
16	14.5	16.2	111.90	248.0	2	9.64	6.4	5.78	192.5	2.4	78.06
23	7.4	13.2	93.84	292.0	1	21.55	6.8	8.96	256.0	3	156.38
Average	12.50	14.07	103.68	288.20	1.40	20.45	7.17	7.92	232.70	2.81	124.73
SD	4.32	1.68	28.34	32.96	0.46	10.6	1.13	3.31	42.06	0.57	55.2
Minimum	7.40	11.70	54.70	247.50	1.00	9.64	5.00	3.77	177.77	2.00	27.47
Maximum	19.60	16.60	155.50	353.80	2.00	46.99	8.50	15.62	319.50	4.00	191.81

sapwood area and Ks at the base, coefficient of determination was 17 and -35 % of correlation with non-linear model (Table 2). These parameters indicate that sapwood area does not influence strongly Ks at base level. However, negative correlation indicates that the little it influences will influence inversely, showing a decrescent curve or line tendency. Crown level Ks related to sapwood area presented statistical parameters of $R^2 = 0.2$ and $r = 0.002$. Therefore, the line and curve tendency is crescent. Since crown segments had smaller diameters, consequently, sapwood area was also smaller than the base. But as we observe Fig. 1a, it is clear that there is a high variation of Ks values ($S = 55.2 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) and probably that is the cause of weak statistical parameter values. Comparing line tendency and data dispersion from base and crown level (Fig. 1a), it is noticeable that sapwood area and Ks present an opposite trend between these levels. Base has a bigger sapwood area range between individuals (maximum 155.5 cm^2), but Ks does not exceed $50 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$. Meanwhile, crown level presented a narrower sapwood area (maximum 15 cm^2), but with Ks practically $200 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$.

Diameter at both levels presented the same tendency as sapwood area. Considering that these variables are directly related, this result was already expected. However, statistical parameters from base level indicate a high coefficient of determination (48 %) meanwhile crown level resulted in a positive (increscent slope) and low (nearly zero) value ($R_{aj}^2 = 0.017$) indicating that diameter barely or does not influence crown Ks as much as base Ks. This result is followed with the same pattern by correlation coefficient,

in which base level was -59 % and crown 13 %. Analyzing both parameters and curve tendency at base level, diameter data are not as disperse as crown data (Fig. 1b) which confirms that at crown level there is little influence from diameter at that height. Base level negative correlation indicates the inversed tendency that diameter has with Ks and the high value of correlation confirms that at base height Ks is significantly influenced by diameter.

The relationship between height and Ks is evident that they possess a different tendency when compared to the other variables (Fig. 1c). Both base and crown level sections presented an increscent tendency ($r_{\text{Base}} = 0.40$; $r_{\text{Crown}} = 0.17$) but low coefficients of determination ($R_{aj\text{Base}}^2 = 0.16$; $R_{aj\text{Crown}}^2 = 0.03$). It is important to highlight that minimum and maximum of Ks values do not correspond to the shortest and tallest palm tree, from this sampling, respectively.

Vessel diameter presented the same tendency as sapwood area. Both levels presented an increscent tendency in which Ks is higher when vessel diameter is also. But, differently from sapwood area, the highest values were at crown level. Base presented a 58 % coefficient of determination and 76 % in correlation (Fig. 1d). Crown presented 79 and 89 %, respectively. These parameters indicate that the variety of vessel sizes present at crown height has a larger influence over hydraulic conductivity. As a counterpoint to vessel diameter, vessel frequency presented a decrescent tendency ($r_{\text{Base}} = -0.013$; $r_{\text{Crown}} = -0.062$) and low statistical parameters for both levels (Fig. 1e). With nearly zero coefficient of determination and correlation ($R_{aj\text{Base}}^2 = 0.054$; $R_{aj\text{Crown}}^2 = 0.007$)

Table 2 Statistical parameters description resulted from linear and non-linear regressions between hydraulic conductivity and palm tree size and anatomical variables

Variables	Level	Model	R^2	r	F	p
Sapwood area × Ks	Base	Linear	0.1232	−0.3510	1.12	$p = 0.320^{ns}$
		Non-linear	0.1756		0.50	$p = 0.635^{ns}$
	Crown	Linear	0.0259	0.1610	0.21	$p = 0.657^{ns}$
		Non-linear	0.0020		0.02	$p = 0.934^{ns}$
Total height × Ks	Base	Linear	0.1633	0.4040	1.56	$p = 0.247^{ns}$
		Non-linear	0.0589		0.51	$p = 0.523^{ns}$
	Crown	Linear	0.0298	0.1726	0.25	$p = 0.633^{ns}$
		Non-linear	0.0189		0.16	$p = 0.915^{ns}$
Diameter × Ks	Base	Linear	0.3454	−0.5877	4.22	$p = 0.074^{ns}$
		Non-linear	0.4879		3.56	$p = 0.095^{ns}$
	Crown	Linear	0.0173	0.1315	0.14	$p = 0.717^{ns}$
		Non-linear	0.0169		0.14	$p = 0.774^{ns}$
Vessel diameter × Ks	Base	Linear	0.5832	0.7764	11.19	$p < 0.001^{***}$
		Non-linear	0.5362		10.09	$p < 0.001^{***}$
	Crown	Linear	0.7889	0.8882	1.83	$p < 0.01^{**}$
		Non-linear	0.7107		2.58	$p < 0.01^{**}$
Vessel frequency × Ks	Base	Linear	0.0540	−0.0126	0.46	$p = 0.478^{ns}$
		Non-linear	0.0685		0.59	$p = 0.380^{ns}$
	Crown	Linear	0.0038	−0.0616	0.03	$p = 0.866^{ns}$
		Non-linear	0.0057		0.05	$p = 0.753^{ns}$

Significance represented by * ($p < 0.05$); ** ($p < 0.01$); *** ($p < 0.001$) and ns for non-significant ($p > 0.05$)

$r_{Base} = -0.012$; $r_{Crown} = -0.062$), it shows that although diameter vessel is highly correlated, their number throughout the cross-section is not as important as conduit size.

Tree hydraulic conductivity

Hydraulic conductivity (Ks) for trees shows an elevated variation between species, especially in wood anatomy dimensions. This was expected since the sampled trees were from various species and ecological succession. Ks varied between 0.09 and 23.35 kg m⁻¹ s⁻¹ MPa⁻¹ with an average of 3.31 ± 4.6 kg m⁻¹ s⁻¹ MPa⁻¹ (Table 3).

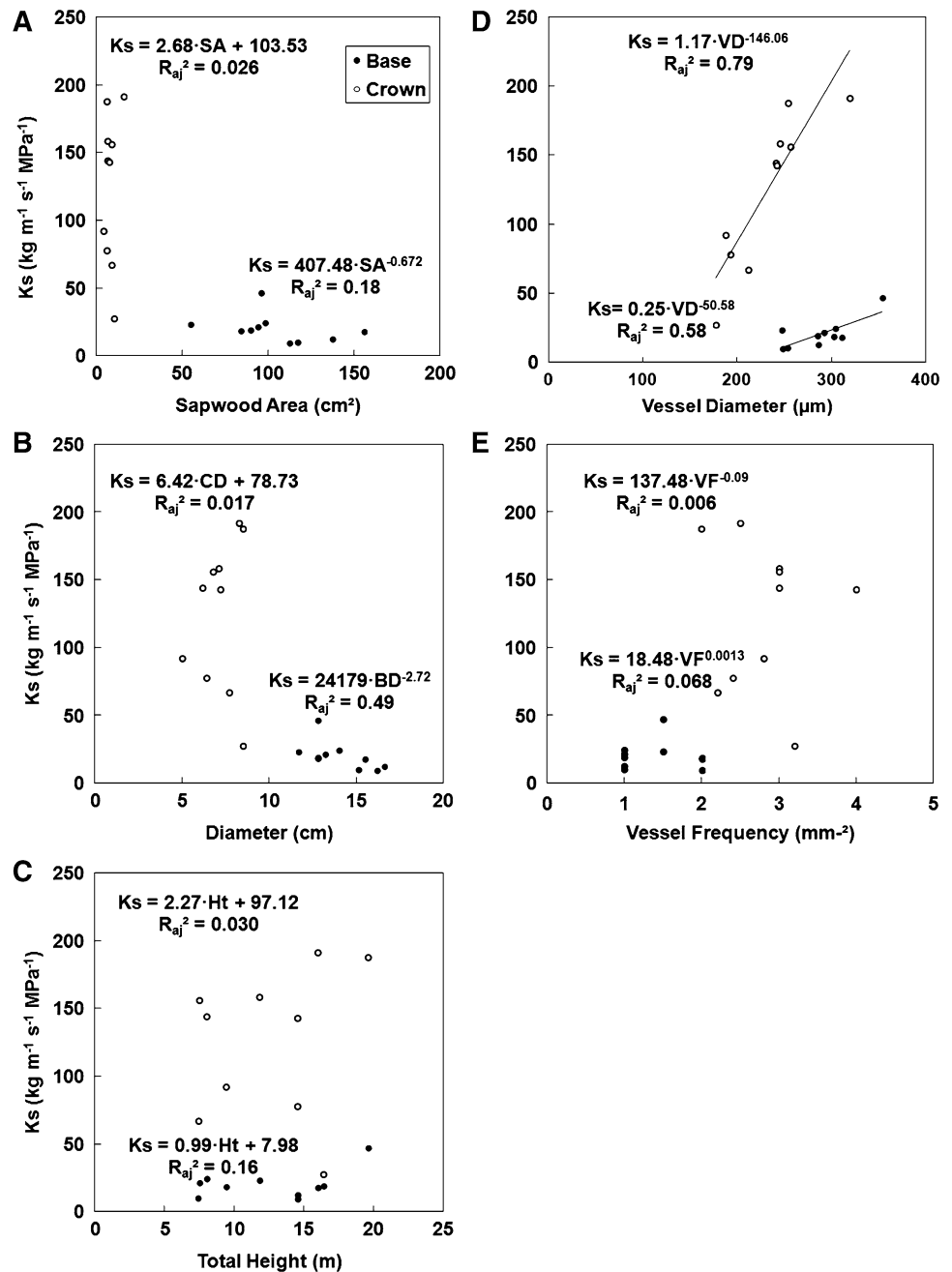
DBH presented low statistical values ($R^2_{ajNLin} = 0.043$; $r = -0.018$) (Table 4) when analyzing its relationship with Ks. These values indicate that this variable does not influence significantly hydraulic conductivity, but that little influence will be decrescent, as larger the diameter, smaller will be the conductivity (Fig. 2a). Total height presented similar results as DBH when analyzing curve tendency and data dispersion (Fig. 2b). Coefficient of determination was nearly 2 % and correlation was 18 %, like DBH, indicating also that hydraulic conductivity is not or barely influenced by tree size. Sapwood area presented superior values than DBH and height ($R^2_{ajNLin} = 0.08$; $r = -0.016$), but

decescent curve tendency was the same (Fig. 2c). These slightly superior values indicate that sapwood area has more influence over hydraulic conductivity considering this is the only variable that delimits and considers the true conductive portion of the tree, while DBH considers the whole cross-section as conductive.

Diameter and vessel frequency presented elevated statistical results ($R^2_{ajVD} = 0.75$; $R^2_{ajVF} = 0.49$) in their relationship with Ks. These variables differentiated specially on coefficient of correlation, where vessel diameter presented an 82 % and vessel frequency −49 % correlation with Ks. These parameters indicate that hydraulic conductivity is extremely influenced by anatomical variables even though these variables presented opposite influence over it (Fig. 2d, e). When an individual presents a large diameter, its frequency will be lower and consequently Ks will be higher.

To confirm this weaker relationship of tree size variables with hydraulic conductivity when compared to anatomical variables, we analyzed ten individuals from the genus *Eschweillera* inside the tree dataset. Species inside the *Eschweillera* genus were the only ones selected for analysis because they possessed the largest number of replicates in the dataset. There were not many species with replicates in our dataset due to the high diversity of species

Fig. 1 Graphs representing non-linear relationship curves between biometrical and anatomical variables with hydraulic conductivity in palm trees. **a** Sapwood area; **b** base and crown diameter; **c** total height; **d** vessel frequency; **e** vessel diameter. *Open symbols* values from the tree base and *open symbols* from the tree crown. *Filled circle* base; *unfilled circle* crown



per hectare in this forest type (Guillaumet 1987; Oliveira and Daly 1999). Tree size variables (DBH, Ht and sapwood area) presented R_{aj}^2 between 9 and 65 % and correlation between -30 and -80 % to K_s ; sapwood area being highly related, but height and DBH again with low relationships. Wood anatomy showed a higher relationship with vessel diameter ($R_{aj}^2 = 0.61$; $r = 0.74$) than vessel frequency ($R_{aj}^2 = 0.05$; $r = -0.22$). Although the statistical parameters obtained from analyzing only one genus were stronger than analyzing a multi-genus dataset, the result

trends still show that anatomical variables are more significantly related to K_s than tree size variables.

Discussion

Conduit properties of palms

Results obtained in this study were similar to others found on other articles about hydraulic conductivity in palm trees.

Table 3 Size, anatomical details and hydraulic conductivity for all sampled trees

N	Species	Family	Total height (m)	DBH (cm)	Sapwood area (cm ²)	Cross-section (cm ²)	Sapwood area/cross-section ratio (%)	Vessel diameter (μm)	Vessel frequency (μm)	Ks (kg m ⁻¹ s ⁻¹ MPa ⁻¹)
1	<i>Cecropia sciadophylla</i> Mart.	Urticaceae	16.50	16.64	214.92	217.47	98.83	232.8	3.1	10.89
2	<i>Eschweilera wachenheimii</i> Sandwith	Lecythidaceae	12.00	10.04	78.38	79.17	99.01	126	8	3.65
3	<i>Vantanea micrantha</i> Ducke	Humiriaceae	21.70	21.08	241.86	349.00	69.30	176.4	3.25	3.06
4	<i>Cecropia sciadophylla</i> Mart.	Urticaceae	15.50	12.48	101.74	122.33	83.17	238	2.5	23.35
5	<i>Cecropia sciadophylla</i> Mart.	Urticaceae	17.55	15.32	182.42	184.33	98.96	210.4	3.2	7.71
6	<i>Virola calophylla</i> (Spruce) Warb.	Myristicaceae	22.50	29.76	648.79	695.59	93.27	87.2	12.3	0.09
7	<i>Cordia silvestris</i> Fresen.	Boraginaceae	19.80	20.60	124.11	333.29	37.24	105.2	5.1	1.12
8	<i>Protium heptaphyllum</i> (Aubl.) March.	Bursaceae	11.20	9.00	36.83	63.62	57.89	80.4	22	1.16
9	<i>Neea madeirana</i> Standl.	Nyctaginaceae	11.25	7.28	41.62	41.62	100.00	58.8	12	0.29
10	<i>Tachigali paniculata</i> Aubl.	Fabaceae— Caesalpinioideae	14.20	8.60	53.86	58.09	92.72	125.6	7.8	4.36
11	<i>Duguetia flagellaris</i> Huber	Annonaceae	13.00	9.20	66.48	66.48	100.00	75.2	11.8	0.47
12	<i>Chrysophyllum ucuquirana-branca</i> (Aubrev & Pellegr) T. D. Penn.	Sapotaceae	20.10	18.04	72.23	255.60	28.26	86	15.1	0.59
13	<i>Ocotea neesiana</i> (Miq.) Kosterm.	Lauraceae	20.00	17.96	76.62	253.34	30.25	100	17.6	1.19
14	<i>Eschweilera wachenheimii</i> Sandwith	Lecythidaceae	22.50	18.40	186.74	265.90	70.23	112	6.9	0.77
15	<i>Virola surinamensis</i> (Rol. Ex. Rottb.) Warb	Myristicaceae	28.50	36.40	950.70	1040.61	91.36	110.4	6.9	0.13
16	<i>Eschweilera wachenheimii</i> Sandwith	Lecythidaceae	19.00	18.16	91.60	259.01	35.36	129.2	6.4	3.33
17	<i>Eschweilera wachenheimii</i> Sandwith	Lecythidaceae	18.00	16.04	44.59	202.07	22.07	139.2	5.8	6.92
18	<i>Mabea caudata</i> Pax & K. Hoffm.	Euphorbiaceae	16.00	10.68	47.50	89.58	53.02	134.4	5.6	5.21
19	<i>Gustavia speciosa</i> (Kunth) DC.	Lecythidaceae	19.00	17.36	133.91	236.70	56.57	66	29.2	0.12
20	<i>Jacaranda copaia</i> (Aubl.) D. Don	Bignoniaceae	25.10	19.72	137.09	305.42	44.89	151.6	3.3	3.38
21	<i>Sclerolobium chrysophyllum</i> Poepp.	Fabaceae— Caesalpinioideae	25.10	21.12	143.19	350.33	40.87	212.4	3.1	9.71
22	<i>Byrsonima crispera</i> A. Juss	Malpighiaceae	16.00	16.28	95.82	208.16	46.03	93.6	17.7	0.61
23	<i>Mabea caudata</i> Pax & K. Hoffm.	Euphorbiaceae	17.15	17.64	152.78	244.39	62.52	126.8	4.95	1.53
24	<i>Vantanea micrantha</i> Ducke	Humiriaceae	23.00	38.44	117.62	1160.53	10.14	136.4	4.7	2.06
25	<i>Brosimum utile</i> (Kunth) Pittier	Moraceae	27.00	26.32	202.98	544.08	37.31	118	6.5	0.80
26	<i>Pourouma guianensis</i> Aubl.	Urticaceae	19.00	26.92	210.83	569.17	37.04	224	2.55	8.07
27	<i>Eschweilera odora</i> (Poepp. ex O. Berg)	Lecythidaceae	22.70	20.70	83.82	334.91	25.03	130.4	5.95	3.36
28	<i>Pouteria cainito</i> Radlk.	Sapotaceae	22.60	25.08	262.75	494.02	53.19	79.6	19.95	0.11
29	<i>Bocageopsis multiflora</i> (Mart.) R. E. Fries	Annonaceae	26.70	26.36	209.85	545.73	38.45	122	6.6	0.90
30	<i>Eschweilera fracta</i> R. Knuth	Lecythidaceae	18.50	21.16	222.17	351.66	63.18	113.2	6.85	0.73

Table 3 continued

N	Species	Family	Total height (m)	DBH (cm)	Sapwood area (cm ²)	Cross-section (cm ²)	Sapwood area/cross-section ratio (%)	Vessel diameter (μm)	Vessel frequency (μm)	Ks (kg m ⁻¹ s ⁻¹ MPa ⁻¹)
31	<i>Micrandropsis scleroxylon</i> W. Rodr.	Euphorbiaceae	28.00	27.32	259.36	586.21	44.24	176.4	4.1	3.47
32	<i>Iryanthera ulei</i> Warb	Myristicaceae	23.20	17.68	192.69	245.50	78.49	82	10	0.20
33	<i>Caliptanthus spruceana</i> Berg.	Myrtaceae	21.00	14.76	108.61	171.10	63.48	76.4	18.5	0.26
34	<i>Eschweilera wachenheimii</i> Sandwith	Lecythidaceae	18.00	13.16	31.79	136.02	23.37	103.2	9.8	3.06
	Average		19.57	18.77	171.36	325.33	58.40	127.62	9.09	3.31
	Standard deviation		4.68	7.43	177.62	258.48	27.02	49.22	6.50	4.59
	Minimum		11.20	7.28	31.79	41.62	10.14	58.80	2.50	0.09
	Maximum		28.50	38.44	950.70	1160.53	100	238	29.20	23.35

Renninger et al. (2013) while analyzing conductivity efficiency in *Iriartea deltoidea* found an average Ks of 24 kg m⁻¹ s⁻¹ MPa⁻¹, which is near the value encountered for our base level estimations. Renninger and Phillips (2010) also analyzed hydraulic conductivity in different heights in palm trees and obtained the same pattern in this present study: low values of Ks at base height and almost four times more at crown height. This indicates that smaller sapwood area leads to a lower hydraulic conductivity.

Therefore, when analyzing hydraulic conductivity (Ks) with diameter and sapwood area, it is observed that both variables have the same tendency for crown (increasing) and base (decreasing). These tendencies are due to palm tree unique diameter growth that will also lead to increase in sapwood area. Palm trees have the same number of vascular bundles throughout the stem and the basal vascular bundles are already ceasing diameter growth cell expansions (parenchyma tissues and fiber stiffening around vascular bundles), but at crown height these tissues and fibers are still expanding and stiffening (Renninger et al. 2013; Waterhouse and Quinn 1978). This was resulting consequently in a narrower sapwood area at this given height (Rich 1987). Palm trees are not characterized by secondary growth (horizontal growth, e.g., diameter) (Huang et al. 2002) and do not form new vascular bundles and new layers of woody tissues such as dicotyledonous trees (Renninger et al. 2013; Tomlinson 1979). According to Rich (1987), *Euterpe macrospadix* [former scientific nomination for *Euterpe precatoria* (Henderson and Galeano 1996)] has a characteristic that is their high capability to stiffen base height cells and according to height growth and aging, thus guarantying strength and firmness in the mechanical support of the stem and crown. Rich (1987) while studying five palm species, among them *Euterpe precatoria*, validated that most species presented smaller vascular bundles at crown height than at base height and that most of them were located in the peripheral area of the cross-section. Further, vascular bundles present near the crown height were denser and consequently indicating that parenchyma cell sizes were smaller at higher sections in the palm stem. Rich (1987) also observed that vascular bundles started sclerifying near the bark first and as the palm individual ages and grows in diameter and height it stiffens vascular bundles located towards the central portion of the cross-section. Thus, the decreasing slope behavior indicates that diameter and sapwood growth results in lower hydraulic conductivity since palm trees will be supplying a certain water volume that before was confined to a small quantity of sclerified vascular bundles through a larger number of mature sclerified vascular bundles in thicker stems. Palm trees do not have the ability of managing its active sapwood area like dicotyledonous trees that results in an overflow on crown height younger

Table 4 Statistical parameters description resulted from linear and non-linear regressions between hydraulic conductivity and tree size and anatomical variables

Variables	Model	R_{aj}^2	r	F	p
DBH × Ks	Linear	0.0339	−0.1842	1.12	$p = 0.297^{ns}$
	Non-linear	0.0428		0.28	$p = 0.532^{ns}$
Total height × Ks	Linear	0.0126	−0.1881	0.41	$p = 0.427^{ns}$
	Non-linear	0.0181		0.22	$p = 0.775^{ns}$
Sapwood area × Ks	Linear	0.0509	−0.1630	1.72	$p = 0.175^{ns}$
	Non-linear	0.0713		2.43	$p = 0.087^{ns}$
Vessel diameter × Ks	Linear	0.6775	0.8231	67.23	$p < 0.001^{***}$
	Non-linear	0.7504		96.24	$p < 0.001^{***}$
Vessel frequency × Ks	Linear	0.2406	−0.4910	10.14	$p < 0.05^{**}$
	Non-linear	0.4938		31.22	$p < 0.05^{**}$

Significance represented by * ($p < 0.05$); ** ($p < 0.01$); *** ($p < 0.001$) and ns for non-significant ($p > 0.05$)

and fewer vascular bundles or excess of mature conduits at base height (Renninger 2010). The increase in conduit surface areas in which water flows will result in stronger friction forces that will cause a reduction in conductivity. The opposite is observed at crown height, where active sapwood area is smaller and consequently there are not enough mature conduits to support the same volume that passed through the base, resulting in an elevation of pressure inside conduits, which results in higher conductivity (in this case, five times the values observed at base height).

As opposed to diameter and sapwood area, height indicated that taller palms presented higher hydraulic conductivity at base and crown levels. But differently from diameter and sapwood increment, height growth continues, even when horizontal cell expansion (“diameter growth”) is stagnating, since palm trees possess a columnar growth characteristic (Salm et al. 2005). Also along with height growth there is increase in crown leaves’ biomass production (Renninger and Phillips 2010). This increase in foliage will result in a higher exposure to solar radiation that will increase the individual’s photosynthetic rate. Another important remark is that taller individuals will have broad crowns that need a higher and more efficient hydraulic conductivity to support leaf petiole embolism at the crown base that can cause around 80 % of hydraulic conductivity loss (Sperry 1985, 1986). Having a higher Ks at crown level than base level shows a hydraulic architecture segmentation that guarantees that the trunk will continue functional although the expendable leaf junction is embolized (Zimmermann 1983; Sperry 1986).

Vessel and diameter frequency presented a tendency already expected when taking palm tree stem anatomy development in consideration. Renninger and Phillips (2010) also documented low Ks values at base height, while vessel diameter was large and frequency was low and the opposite was observed at crown height. That is attributed to the fact that palms cannot adjust their

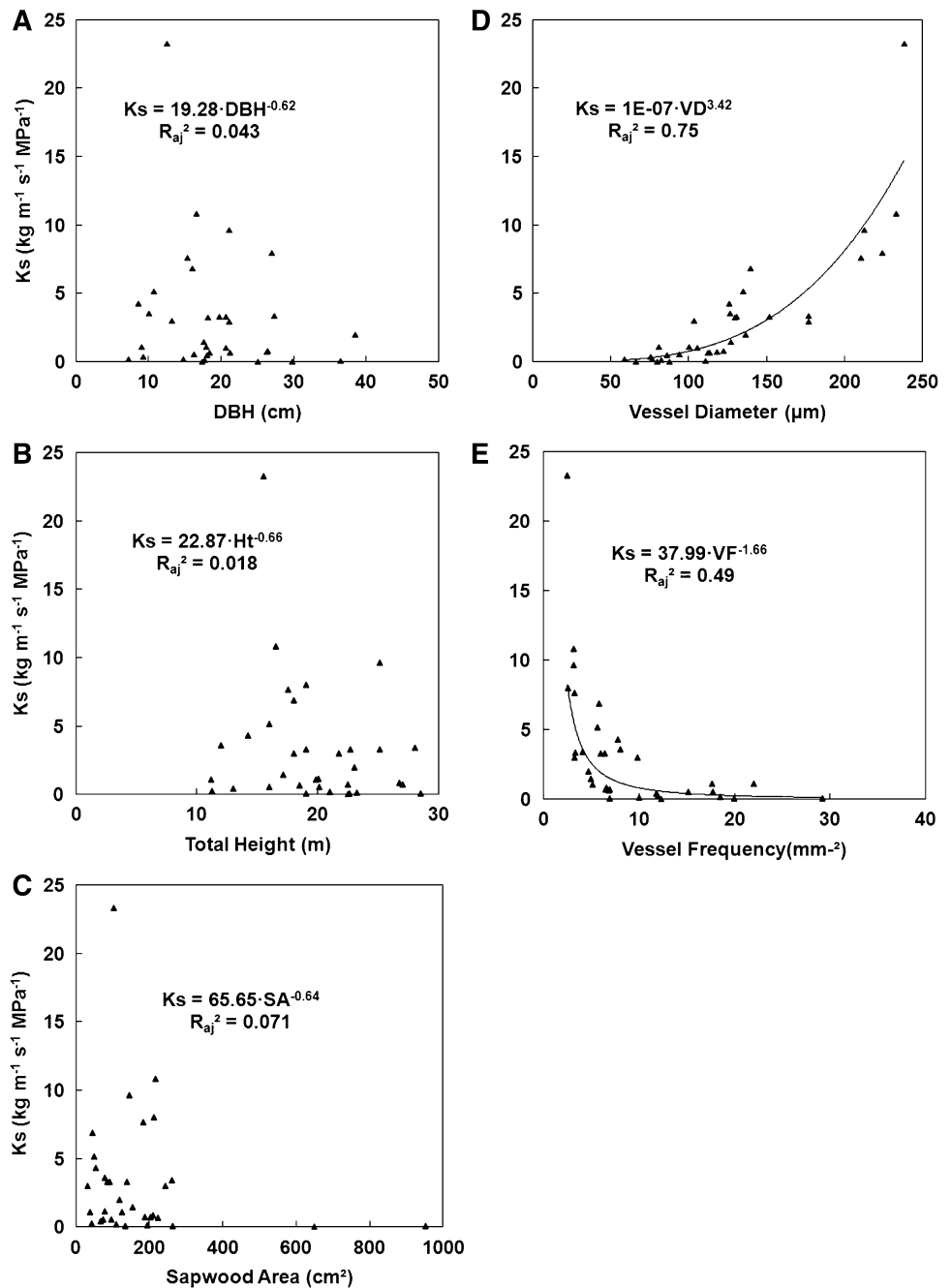
conductive system through new vascular bundle formations according to its growth and habitat. Instead, vascular bundles mature with time, which results in more sclerified bundles that will increase mechanical stability for a more efficient water ascent.

Conduit properties of tropical trees

Hydraulic conductivity values found in this study are consistent with results found in other studies with dicotyledonous trees. Vinya et al. (2012) obtained Ks ranging from 5.74 to 24.19 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ when studying nine African tree species; and Dettmann et al. (2013) obtained 1.8 and 10.5 with four species at high altitudes in Chile $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$.

Based on our results, tree size variables (DBH and total height) have little or no influence over hydraulic conductivity, even though sapwood area and Ks were an exception being highly correlated when analyzed inside the *Eschweillera* genus. Despite other authors indicate that tree size does have a significant influence over Ks (Rosner et al. 2008; McCulloh et al. 2010), others presented similar results to this study. Simonin et al. (2006) while studying effect of forest stand thinning through hydraulic conductivity and tree size in *Pinus ponderosa* stands, the authors found the same decrescent slope tendency found in tree height and sapwood area. They believe that this is due to difference in age within the same species stand. Domec and Gartner (2003) reported a decrescent relationship between Ks and sapwood area and DBH. This study believes that lack of control from secondary growth over embolism and cavitation or other conduit obstruction caused low values of Ks. Both theories presented can be applied to this present study. There was a high occurrence of tyloses on the sampled trees (50 %) and the stand in which the samples were collected is highly probable to have a large age variation between

Fig. 2 Graphs representing non-linear relationship curves between biometrical and anatomical variables with hydraulic conductivity in trees. **a** Sapwood area; **b** DBH; **c** total height; **d** vessel frequency; **e** vessel diameter



the individuals. Age was not estimated for this study, but since the study site is located inside a primary Amazon forest, it is right to assume that there are old and young trees in this sampling. The reason for the K_s declination due to growth stagnation is that carbon assimilation starts to reduce. Consequently, water use is also reduced. The assimilated carbon in older trees is then invested in xylem conduit stiffness and not in diameter, sapwood and height growth (McCulloh et al. 2011).

Vessel diameter and frequency presented a strong influence over hydraulic conductivity. This relationship with

K_s and vessel diameter or frequency was also reported by other authors, like McCulloh et al. (2010) that studied hydraulic efficiency in different wood porous trees. This opposite relationship between conduit diameter and frequency is also well known throughout hydraulic architecture and/or wood anatomy literature, where various authors with various species, location and functional groups concluded that when there are large porous they are less frequent (McCulloh et al. 2010; Renninger et al. 2013; Zach et al. 2010; Fan et al. 2012; Tyree et al. 1992). Large and little distributed vessels normally are associated to higher

conductivity and more efficient than narrower and smaller vessels (Zanne et al. 2010).

This increscent relationship between vessel diameter and Ks is evident in individuals 1, 4 and 5 (all *Cecropia sciadophylla*), which all have large vessels, low frequency and extremely high Ks values compared to the other individuals in this sampling. Meanwhile, lower values were observed in individuals with small porous and high frequency (e.g., individual no. 13- *Ocotea neesiana*). This variability found between sampled individuals matches the variety of ecological succession stages. The individuals that presented the highest Ks are species classified as pioneers and lowest as secondary. Besides *Cecropia sciadophylla*, *Eschweillera wachenheimii* (no. 17) (Lima et al. 2002), *Mabea caudata* (no. 18) (Lorenzi 1992), *Sclerobium chrysophyllum* (no. 21) and *Pourouma guianensis* (no. 26) (Maranho and Paiva 2012) were other pioneer trees that presented high Ks which matched to large vessels (over 130 μm) and low frequency (between 2.5 and 5.8/ mm^{-2}). It is important to highlight that these species are similar only in these variables. Tree size variables vary significantly between them. According to McCulloh et al. (2011), pioneer trees are considered hydraulically efficient since they are able to invest the assimilated carbon rapidly for biomass production, since these types of trees possess a fast growth characteristic.

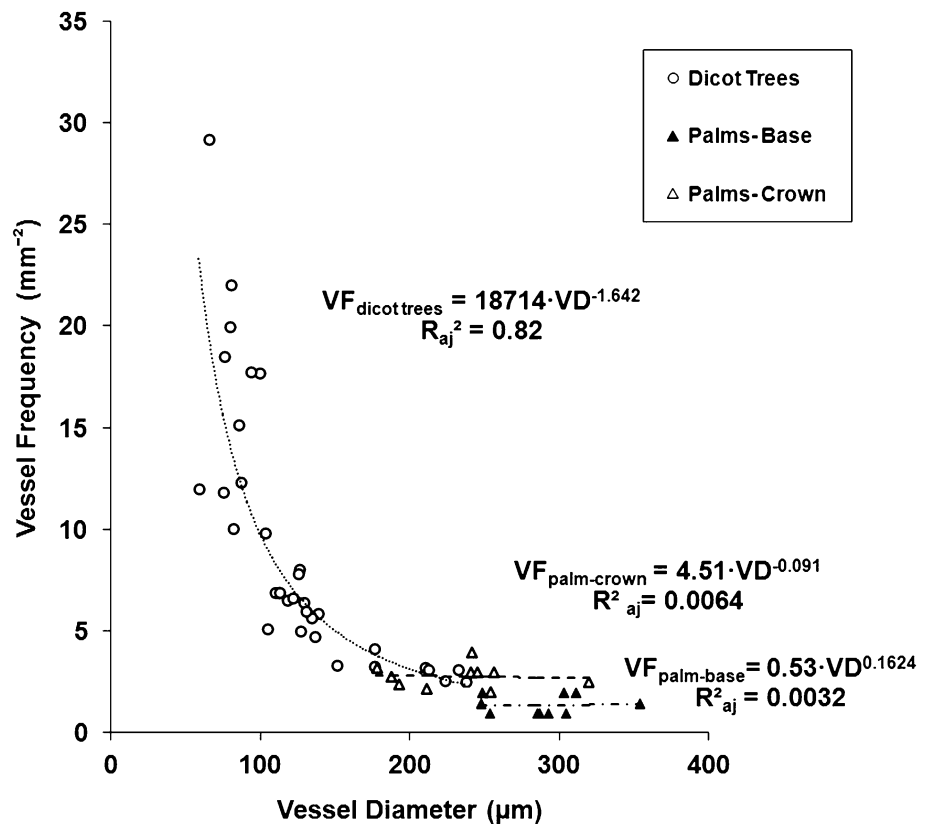
Poorter et al. (2010) explained that since pioneer species are more exposed to solar radiation, they have higher photosynthetic rates that supply the necessary carbon quantity needed for their rapid growth. This supply is only possible through an efficient and high hydraulic conductivity. Thus, to comprehend how hydraulic conductivity is influenced in trees, it is important to relate their wood anatomy to their ecological behavior.

Tree and palms: comparison

Although palm trees are anatomically different from trees, when we analyze vessel diameter and frequency, both presented inverse relation between each other for both functional groups (Fig. 3). This pattern has been found in various studies and can be considered as a global pattern for woody plants that possess similar wood features to dicot and monocot trees focused on this present study (e.g. Diffuse porous arrangement). (Zanne et al. 2010; McCulloh et al. 2010; Renninger et al. 2013; Zach et al. 2010; Fan et al. 2012; Tyree et al. 1991).

The most significant difference between trees and palm trees was the higher values of Ks for palm tree base values ($\text{VD}_{\text{MaxBase}} = 46.99 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) than in tree DBH measurements ($\text{VD}_{\text{MaxDBH}} = 10.89 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$). These higher values indicate that palms are

Fig. 3 Conduit diameter (μm) vs. conduit frequency (mm^{-2}) for Amazonian trees and *Euterpe precatoria* palms



hydraulically more efficient plants than dicot trees. In other words, palm trees invest more assimilated carbon in the production of leaves than producing new vascular bundles and/or woody tissues and branches like trees (Cruziat et al. 2002).

Another factor to consider about the difference between palms and trees is the capacity of trees to adapt their conductive area according to their microclimate and seasonal adaptations and the occurrence of embolism and cavitation. Palms are less affected by embolism and cavitation than trees (Sperry 1985, 1986; Zimmermann 1983), therefore lacking a conduit regeneration capacity, making them hydraulically more efficient even with high water use and stronger, longer and stiffer conduits. But this hydrological advantage also compromises palm trees' geographical distribution being limited to certain areas (Tomlinson 2006; Gomes and Prado 2007), like *Euterpe precatoria* that only occurs in flooded regions of the Amazon where water is more available in the soil than in higher terrains (Kunert et al. 2013).

Conclusions

This study highlights the structural difference between trees and palms in their vascular anatomy both representing a unique strategy to maintain water transport in the same environmental settings. Trees grow new active xylem and inactivate older xylem, whereas palms, characterized by missing secondary growth, need to maintain their vascular tissues by stiffening and thus achieving a high hydraulic efficiency. This difference in initial investment into vessels is resulting in much smaller vessels and higher vessel frequency in trees than in palms. Despite the structural differences between both plant types, we found some functional convergence as the relationship between vessel frequency and diameter is following a common function between the two plant groups. Palms need a large amount of water and carbon to constantly produce leaf biomass and facilitate conduit stiffening. High hydraulic efficiency plays an important role during times with less soil water availability and high evaporative demand, since palm trees are more vulnerable to embolism under those conditions. Along with the vascular advantage, palms occur in moist and shaded areas in the Amazon characterized by a high ground water table even in the dry seasons. Also, the capacity of palms to control stomata closure also creates an ideal condition for conduit integrity.

Author contribution statement Aparecido, L. M. T.: material and data collector (handling harvested tree logs, tree species identification, dye immersions (trees and palms), sapwood area determination and wood anatomy

laboratory analysis); data processing (database organization and processing, hydraulic conductivity estimation, statistical analysis, graphs and figures formatting); main writer; and project proposition and main concept developer. dos Santos, J.: served as scientific advisor; logistics coordinator and writing reviser. Higuchi, N.: served as scientific advisor; Forest Management Laboratory—INPA coordinator that provided: field workers for tree and palm harvesting, storage space for material collection, and office space for data analysis and writing; and writing reviser. Kunert, N.: served as scientific advisor; material and data collector (tree and palm harvesting and handling); transportation and equipment/material provider (for field work and laboratory analysis); main reviser (material and data processing, results and discussions, and initial to final manuscript draft) and secondary writer (contributions to the draft); project proposition and secondary concept developer.

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Conflict of interest The authors declare that they have no conflict of interest.

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