Tree height effects on vascular anatomy of upper-canopy twigs across a wide range of tropical rainforest species

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Abstract

Vessel diameter variation along the hydraulic pathway determines how much water can be moved against the force of gravity from roots to leaves. While it is well-documented that tree size scales with vessel diameter variation at the stem base due to the effect of basipetal vessel widening, much less is known whether this likewise applies to terminal sun-exposed twigs. To analyze the effect of tree height on twig xylem anatomy, we compiled data for 279 tropical rainforest tree species belonging to 56 families in the lowlands of Jambi Province, Indonesia. Terminal upper-canopy twigs of fully grown individuals were collected and used for wood anatomical analysis.

We show that hydraulically weighted vessel diameter (D_h) and potential hydraulic conductivity (K_p) of upper canopy twigs increase with tree height across species although the relationship was weak. When averaged across given tree height classes irrespectively of species identity, however, a strong dependency of tree height on D_h and K_p was observed, but not on the lumen-to-sapwood area ratio (A_l:A_x) or vessel density (VD).

According to the comparison between actual tree height and the maximum tree height reported for a given species in the stand, we show that the vascular xylem anatomy of their terminal twigs reflects their canopy position and thus ecological niche (understory versus overstory) at maturity. We conclude that the capacity to move large quantities of water during the diurnal peak in evaporative demand is a prerequisite for growing tall in a humid tropical environment.

1. Introduction

To ensure high growth performance in plants, a continuous and reliable water supply to photosynthetically active organs is essential. Long-distance water transport in trees occurs along the soil–plant–atmosphere continuum that creates a continuous pathway of liquid water extending from the roots to the leaves (Tyree & Zimmermann 2002). Along this gradient, water is moved by following the descending water potential gradient through an interconnected network of xylem conduits (Lambers *et al.* 2008). The efficiency of this network to transport water varies between tree species and depends on their plant hydraulic architecture (Kotowska *et al.* 2015, Olson *et al.* 2018, Schuldt *et al.* 2013). Along this hydraulic pathway, hydraulic efficiency and thus the resistance of a given segment is described by the potential hydraulic conductivity (K_p), which depends on the number and diameter of vessels per cross-section as hydraulic conductivity scales with the fourth power according to the Hagen–Poiseuille equation (Tyree & Ewers 1991, Tyree & Zimmermann 2002). To increase hydraulic conductivity, plants might therefore enhance the vessel lumen fraction, i.e. the lumen-to-sapwood area ratio (A_l:A_x), by either producing larger vessel diameters or by increasing the number of vessels, or both.

How high water needs to be transported to reach the leaves thereby plays a critical role in the construction, structure and stability of the hydraulic network as large stature poses challenges for trees, both from a mechanical and hydraulic perspective (Larjavaara 2014, Ryan & Yoder 1997). Accordingly, tree height has substantial implications for other plant functions, such as canopy and stem dimensions (Sterck & Bongers 2001, Larjavaara 2014), leaf area index and water use (Falster *et al.* 2011, Horna *et al.* 2011) as well as carbon gain and storage (Feldpausch *et al.* 2012, Kotowska *et al.* 2021), but also drought-induced mortality

(Bennett *et al.* 2015, O'Brien *et al.* 2017). Because top canopy trees tend to receive a higher light intensity than their smaller neighbours (Cavaleri *et al.* 2010), tree height seems more important in terms of competitive fitness than standing biomass (Falster *et al.* 2003). This facilitates a disproportionate share of resources, which increases their competitiveness (Feng *et al.* 2019, Toldi *et al.* 2019, Weiner 1990), while shorter trees may have greater adaptation capacity and higher drought resistance (Fajardo *et al.* 2019). On the other hand, large stature poses several challenges for trees. While taller trees are more wind-exposed and thus more vulnerable to breaking (Jackson *et al.* 2020), water transport from roots to the leaves is increasingly challenged by gravity and path-length resistance.

While wide and conductive vessels allow greater rates of sap movement (Kotowska *et al.* 2021), they also leave more space for fibres, which mainly serve for mechanical support (Chave *et al.* 2009, Martínez-Cabrera *et al.* 2011, Ziemińska *et al.* 2013). This might trade-off with the density of the woody tissue, and in fact wood density has been associated with vessel features and thus water transport capacitance in various ecosystems (Hoeber *et al.* 2014, Pfautsch *et al.* 2016, Preston *et al.* 2006). Hard-wooded trees have often been associated with greater hydraulic safety, longevity and reduced growth rate, while fast growth comes at the cost of elevated mortality risk due to hydraulic failure and lower resistance to environmental hazards and pathogens (e.g. Eller *et al.*, 2018, King *et al.*, 2006; Kraft *et al.*, 2010). In evergreen wet tropical forests, on the other hand, wood density was found to vary independent of any hydraulic trait (Baraloto *et al.* 2007, Fan *et al.* 2012, McCulloh *et al.* 2010, Schuldt *et al.* 2013), with tree size and hydraulic efficiency playing the major role for carbon gain and water use (Kotowska *et al.* 2021). Therefore, hydraulic efficiency has been identified as the pivotal role in terrestrial plant productivity from the individual tree to the ecosystem level (Brodribb 2009).

As trees grow tall, they are thus facing hydraulic limitations, which might result in reduced transpiration and lower photosynthesis rates resulting in reduced growth (Ambrose *et al.* 2018, Koch *et al.* 2004, Ryan & Yoder 1997). To ensure sufficient water transport to the upper leaves, the development of an optimal well-adapted water flow pathway is therefore required in order to support the potential maximum tree height and water demand a given species can reach. Because the terminal twigs are exposed to the steepest gradients in evaporative demand and the highest gravitational force and friction, narrow conduits seem advantageous in order to prevent hydraulic dysfunction (Olson *et al.* 2018). As a consequence, basipetal conduit widening from the apex towards the stem base is a universal pattern, and tall trees consequently have larger vessels at the stem base than smaller trees to allow for high flow rates (Fang *et al.* 2013, Kotowska *et al.* 2021, Olson *et al.* 2014, 2020, Poorter *et al.* 2010, Toft *et al.* 2019). This tip-to-base conduit diameter widening with tree height was predicted by hydraulic optimality models (West *et al.* 1999) and reported to follow a power law throughout many studies (Anfodillo *et al.* 2006, Coomes & Allen 2007, Olson *et al.* 2021, Petit *et al.* 2010, Petit & Crivellaro 2014, Rosell *et al.* 2017). In contrast, the adjustments of hydraulic traits at the upper canopy in relation to the actual and potential tree height a species can reach are less documented, but available studies indicate that vessel diameters in sun-exposed top canopy branches increase with height, mainly across species (Kotowska *et al.* 2015, Liu *et al.* 2019, Olson *et al.* 2014, 2021, Schuldt *et al.* 2013, Zach *et al.* 2010). At first glance, this seems to contradict the assumption that hydraulic efficiency

Table 1. Stand characteristics for all trees with DBH >10 cm for the two landscapes Harapan (HR) and Bukit 12 (BD) measured in 2019. Given are mean values ± SD for the four plots per landscapes

Structural variable	HR	BD
Mean tree height (m)	23.71 ± 0.52	18.29 ± 1.96
Max. tree height (m)	51.87 ± 2.15	44.73 ± 1.53
Mean DBH (cm)	21.38 ± 1.13	23.53 ± 2.21
Wood density (g cm^{-3})	0.572 ± 0.013	0.554 ± 0.022
Stem density (n ha^{-1})	593 ± 86.7	368 ± 40.3

must decline vertically in order to compensate for the increase in gravitational force and resistance friction with height (Burgess *et al.* 2006, Halis & Djehichi 2012). Indeed, Woodruff *et al.* (2008) observed a linear intra-specific decline in vessel diameters in upper-canopy branches with height in a tall-growing conifer, but comparable data are scarce.

In order to test whether the tree height and canopy position a given species may reach at maturity influences hydraulics traits of terminal twigs of tropical angiosperm trees, we collected sun-exposed samples from the uppermost canopy of 279 tree species from a phylogenetically and structurally diverse Indonesian lowland rainforest. We analysed the influences of actual (H) and maximal tree height (H_{max}), diameter at breast height (DBH) and stem wood density (WD) on wood anatomical and derived hydraulic traits in these terminal twigs. We hypothesized that (i) trees from tall species have disproportionately wider vessels in the upper-most canopy branches to optimize for maximal conductive demand, (ii) while their mechanical stability expressed as wood density is unrelated to vessel sizes and does not trade-off with hydraulic conductance in this humid tropical environment.

2. Materials and methods

2.1. Study sites and macroclimate conditions

The research was carried out in two tropical lowland rainforests remnants (50–60 m a.s.l) of Jambi Province, Sumatra. The study sites are located in two protected areas: Harapan rainforest (HR) of Muara Bulian Regency (S 2°0′ E 103°24′) and Bukit Duabelas National Park (BD) of Sarolangun Regency (S 1°56′ E 102°34′). Both protected areas correspond to former logging concessions and have been protected for more than 20 years. The forests can be considered as logged-over primary lowland forest. Stand characteristics measured in 2019 for all trees with a DBH >10 cm did not differ between the two landscapes (HR and BD, respectively) ($t = -0.36$, $p > 0.05$, Table 1). Acrisols are the dominant soils in both sites, with clay texture in BD and a sandy loam texture in HR (Allen *et al.* 2015). The climate is moist tropical with a mean annual precipitation of 2,552 mm yr^{-1}, a mean daily temperature of 24°C and 25.3°C, and a mean daily relative humidity of 92% and 90% at BD and HR sites, respectively (Drescher *et al.* 2016).

2.2. Tree selection and height measurements

The twig samples were collected at eight 50 m × 50 m forest inventory plots at each location from tree individuals with a DBH ≥ 10 cm. We aimed at sampling one mature individual of each species, which represents the maximum height reached by
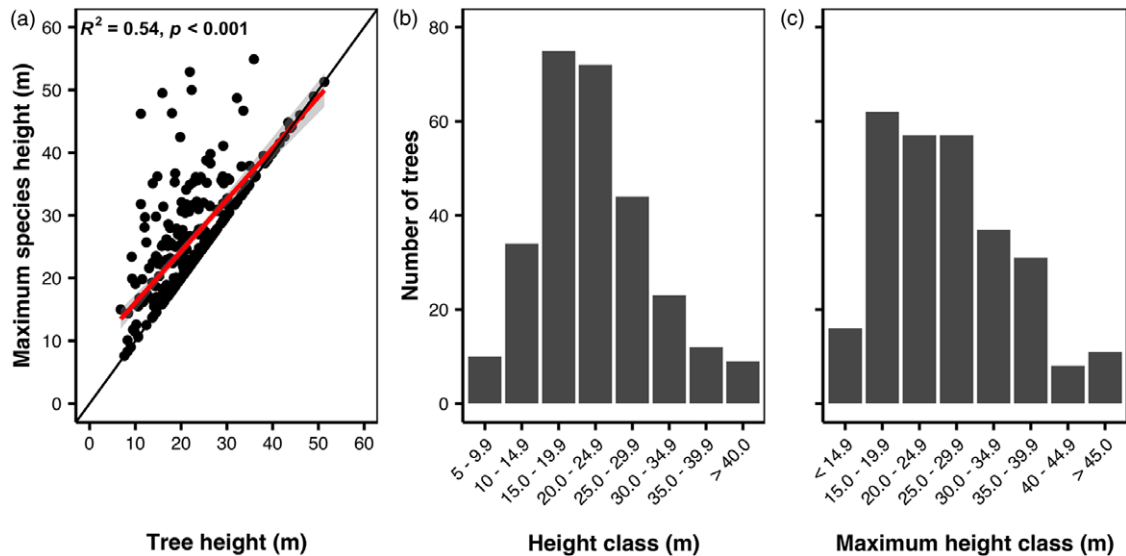
Figure 1. Linear regression analysis between actual and reported maximum height for the 199 tropical tree species from lowland forests on Sumatra (a), as well as histograms showing the number of species per selected tree height class for actual tree height (b) and maximum tree height (c).

that species across all plots. In total, 279 species belonging to 142 genera and 56 families were sampled (Table S1). Due to logistic reasons, however, it was not always possible to sample the tallest individual per species. We therefore additionally estimated the maximum height of all tree species from our inventory data covering 3517 forest tree individuals in total. Across our species sample, actual tree height (H, m) and maximal tree height (H_{max}, m) were highly interrelated (Fig. 1), and in most cases we indeed managed to collect samples from the tallest individuals. Sun-exposed upper-canopy branches were collected by using a slingshot (Big Shot, Notch Equipment, USA) to pull up a hand chain saw (RoNa, Düsseldorf, Germany) for cutting-off the branch. Across all species, similar-sized twigs with a diameter of 8.84 ± 1.61 mm (mean ± SD) were selected and stored in 70% ethanol for subsequent wood anatomical analysis. Tree height was measured using a Vertex III height meter (Haglof, Sweden).

2.3. Vessels anatomy and potential hydraulic conductivity

The complete samples were sectioned using a sliding microtome (G.S.L.1, WSL Bismendorf, Switzerland). The resulting semi-thin cross-sections were stained using a mixture of 0.65% alcian blue and 0.35% safranin (w/v), and subsequently digitalized using a stereo-microscope with an automatic stage equipped with a digital camera (SteREOV20, Carl Zeiss MicroImaging GmbH).

Image processing was done with the software Adobe Photoshop CS6 (Adobe Systems Inc., U.S.A.) and ImageJ v1.5.2. for analyzing the diameter and number of all xylem vessels in the complete cross-section by the automated particle analysis function and to calculate the corresponding xylem area. All vessels of a cross-section (xylem area mean ± SD: 45.4 ± 24.0 mm^2) were analyzed, yielding 600–20,000 measured vessels per sample. We estimated vessel diameter (D, μm) from major (a) and minor (b) vessel radii according to $D_i = ((32 \times (a \times b)^3)/(a^2 + b^2))^{1/4}$ (White & Majdalani 1999), the hydraulically weighted vessel diameter (D_h) according to $D_h = \Sigma D_i^5/\Sigma D_i^4$ (Sperry & Saliendra 1994), vessel density (VD, n mm^{-2}) and the lumen-to-sapwood area ratio (A_l:A_x, in percentage; see Table 2 for descriptions). As the flow rate of water along a

tube is proportional to the fourth power of its radius, a small increase in conduit diameter causes a substantial increase in flow rate or conductivity (Sperry *et al.* 2006). The hydraulically weighted vessel diameter corresponds to the lumen of average Hagen–Poiseuille conductivity for the sampled cross-section area and thus is a better predictor of hydraulic conductivity than the non-weighted mean vessel diameter (Hacke *et al.* 2017). We further calculated the potential hydraulic conductivity (K_p, kg m^{-1} MPa^{-1} s^{-1}) of the twig xylem based on the Hagen–Poiseuille's law as $K_p = \pi \times \rho \times \Sigma(D_i^4)/(128 \eta \times A_{xylem})$, where D_i is the diameter of each single vessel i, η the water viscosity (1.002×10^{-9} MPa s) and ρ the density of water (998.2 kg m^{-3}), both at 20 °C, and A_{xylem} (m^2) the analyzed sapwood area.

2.4. Statistical analyses

Statistical analyses were performed using *R* software version 3.6.1 (R Core Team 2019) and the packages corrmorant (Link 2020), ggplot2 (Wickham 2016), and ggpubr (Kassambara 2020). We investigated the effect of tree height on hydraulically weighted vessel diameter (D_h), VD, lumen-to-sapwood area ratio (A_l:A_x) and potential hydraulic conductivity (K_p) of twigs using linear regression analyses. We additionally grouped given species according to their measured actual tree height (H) and documented maximum tree height per species in the region (H_{max}). We created eight tree height classes for H (5.0–9.9 m, $n = 10$; 10.0–14.9 m, $n = 34$; 15.0–19.9 m, $n = 75$; 20.0–24.9 m, $n = 72$; 25.0–29.9 m, $n = 44$; 30.0–34.9 m, $n = 23$; 35.0–39.9 m, $n = 12$; >40.0 m, $n = 9$) and eight tree height classes for H_{max} (<14.9 m, $n = 16$; 15.0–19.9 m, $n = 62$; 20.0–24.9 m, $n = 57$; 25.0–29.9 m, $n = 57$; 30.0–34.9 m, $n = 37$; 35.0–39.9 m, $n = 31$; 40.0–44.9 m, $n = 8$; >45.0 m, $n = 11$). For a linear regression analysis across height classes, H or H_{max} and the variable of interest was averaged, ignoring the unbalanced species number per height class. A first inspection of the dataset was done with the help of the correlation matrix shown in Fig. S1, and linear regression analyses were used to identify a significant effect of tree height on the variable of interest. Kruskal–Wallis test were performed to test whether height classes differ

Table 2. List of tree structural and twig wood anatomical variables with definition and units employed.

Variables	Unit	Definition
H	m	Tree height
DBH	cm	Tree diameter at 1.3 m breast height
WD	g cm^{-3}	Wood density as ratio of oven-dry mass by green volume
d	µm	Mean vessel diameter
Dh	µm	Hydraulically weighted vessel diameter
VD	n mm^{-2}	Vessel density
Kp	kg m^{-1} MPa^{-1} s^{-1}	Potential sapwood area-specific hydraulic conductivity
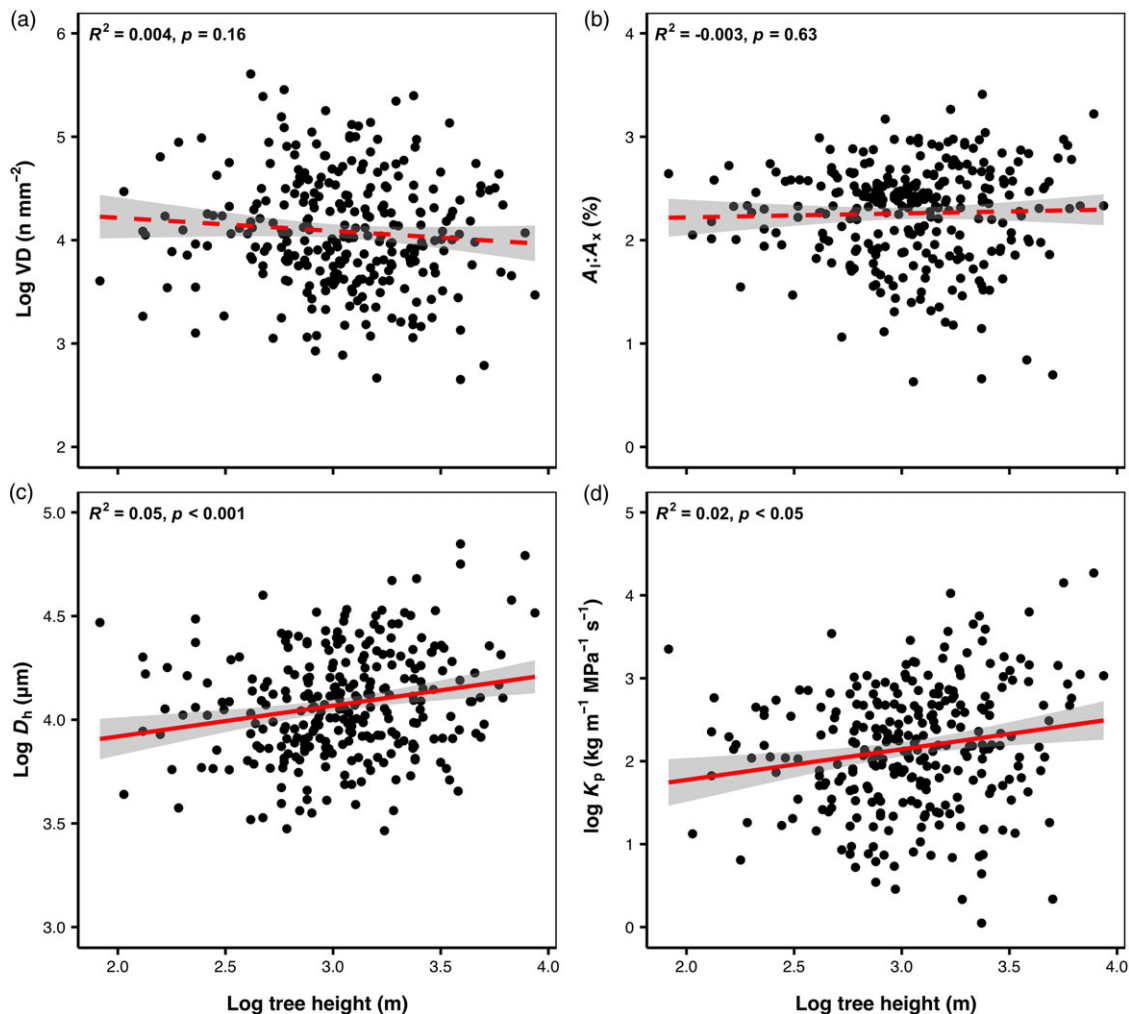
Figure 2. Actual height of the 279 tropical rainforest species in relationship to vessel density (a), hydraulically weighted vessel diameter (c), and potential hydraulic conductivity (d). Red lines are regression curves of linier regression model (a, c, d) while dashed line represents a non-significant influence (b). Grey areas show the 95% confident interval of the models.

significantly from each other for the hydraulic trait of interest. Non-normally distributed data were log-transformed.

3. Results

Across the 279 tropical rainforest tree species of our sample, actual tree height (H) was closely related to the maximum tree height (H_{max}) reported for a given species, and to their DBH (Figure 1a, Figiure S1). Although we observed quite a variability across species and a low coefficient of determination, D_h and K_p of terminal twigs increased significantly with tree height ($p < 0.001$ and $p < 0.05$, respectively) (Fig. 2). We found no effect of tree height on VD and lumen-to-sapwood area ratio (Fig. 2). According to the linear regression analysis, log transformed D_h and K_p were increasing with tree height by 0.64 µm and 0.34 kg m^{-1} MPa^{-1} s^{-1} per meter across species, respectively.
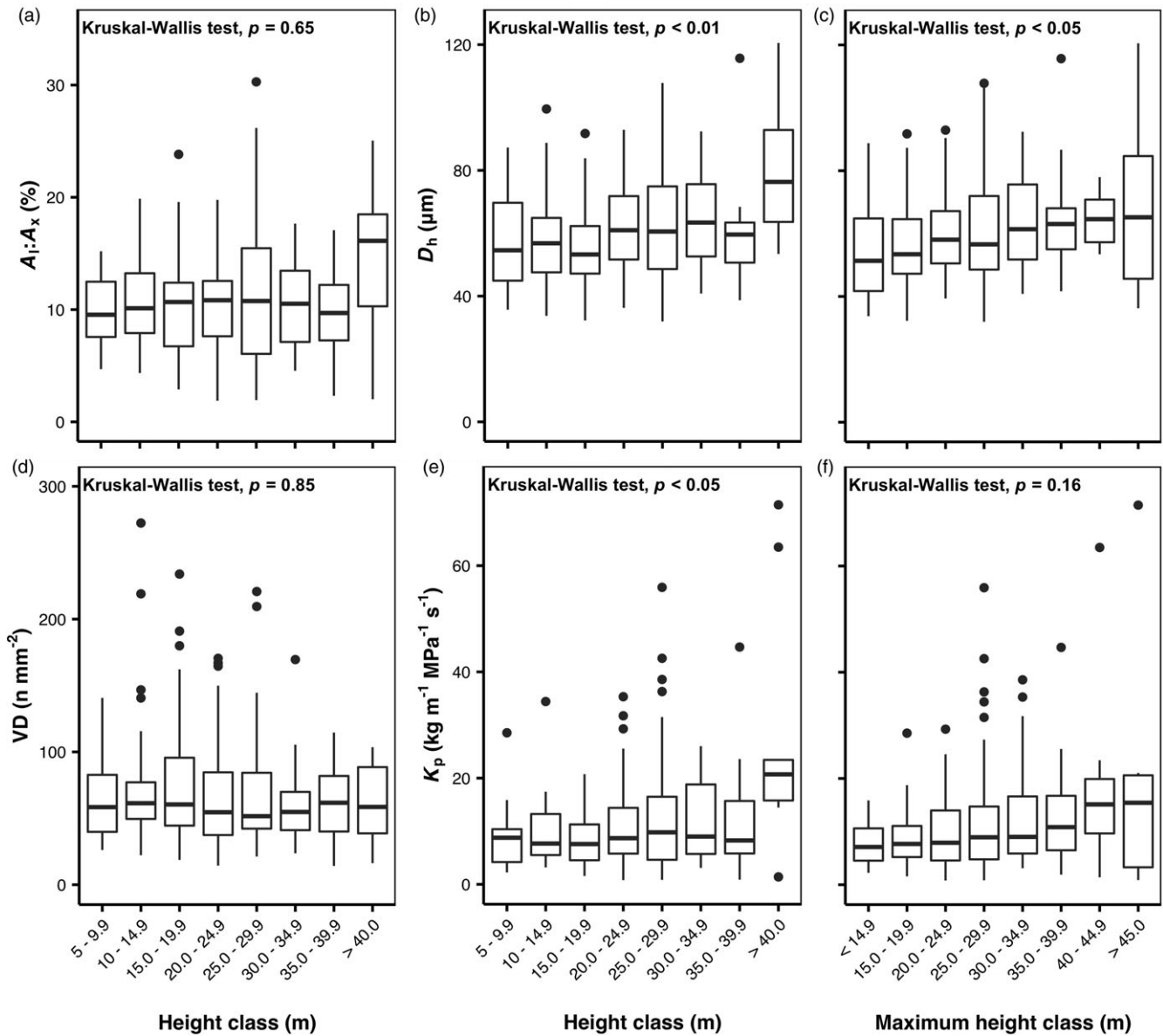
Figure 3. Differences of hydraulic traits across aggregated actual tree height classes for the lumen-to-sapwood area ratio (a), hydraulically weighted vessel diameter (b), vessel density (d) and potential hydraulic conductivity (e), as well as the hydraulically weighted vessel diameter (c) and potential hydraulic conductivity (f) across tree height classes based on the maximum tree height of a given species in the region.

In addition to the actual height of a given tree (H), D_h and K_p likewise increased with the maximum height (H_{max}) of the species ($R^2 = 0.05$, $p < 0.001$ and $R^2 = 0.02$, $p < 0.01$, respectively). Unlike with the actual tree height, we found that VD decreased ($R^2 = 0.01$, $p < 0.05$) with H_{max} (Fig. S2). As with the actual height, no correlation was observed between A_l:A_x and H_{max} ($R^2 < 0.01$, $p = 0.31$).

When pooled across species within their given tree height class, D_h and K_p likewise differed significantly between height classes according to a Kruskal–Wallis test ($p < 0.01$ and $p < 0.05$, respectively; Fig. 3). Ignoring the variable number of species per tree height class (refer to Figure 1b, c), a linear regression analysis between mean tree height per height class likewise revealed a strong relationship for both D_h and K_p ($R^2 = 0.68$, $p < 0.05$ and $R^2 = 0.60$, $p < 0.05$, respectively; Fig. S3). This relation became even stronger for categories created according to the mean maximal tree height per height class documented for each species in

the region against D_h and K_p ($R^2 = 0.75$, $p < 0.001$ and $R^2 = 0.85$, $p < 0.001$, respectively). However, when accounting for each class variance, Kruskall–Wallis test was non-significant in the case of Kp across H_{max} classes. According to the regression analysis across the mean of each classes, hydraulically weighted vessel diameters increased from 53.9 ± 4.0 μm at 11.8 ± 0.6 m H_{max} to 79.3 ± 15.0 μm at 42.6 ± 0.6 m H_{max} (mean ± SE), i.e. D_h increased by 0.82 μm per meter across species (data not shown). In contrast, no significant differences between height classes with respect to VD and A_l:A_x were found (Fig. 3).

We further observed a weak but highly significant relationship between D_h and the stem DBH as well as WD (Fig. 4). The latter remained significant even after excluding the two most light-wooded species. Although the r-square values are likewise low across the 279 tree species ($R^2 < 0.1$), D_h increased ($p < 0.01$) while WD declined ($p < 0.01$) with increasing height.
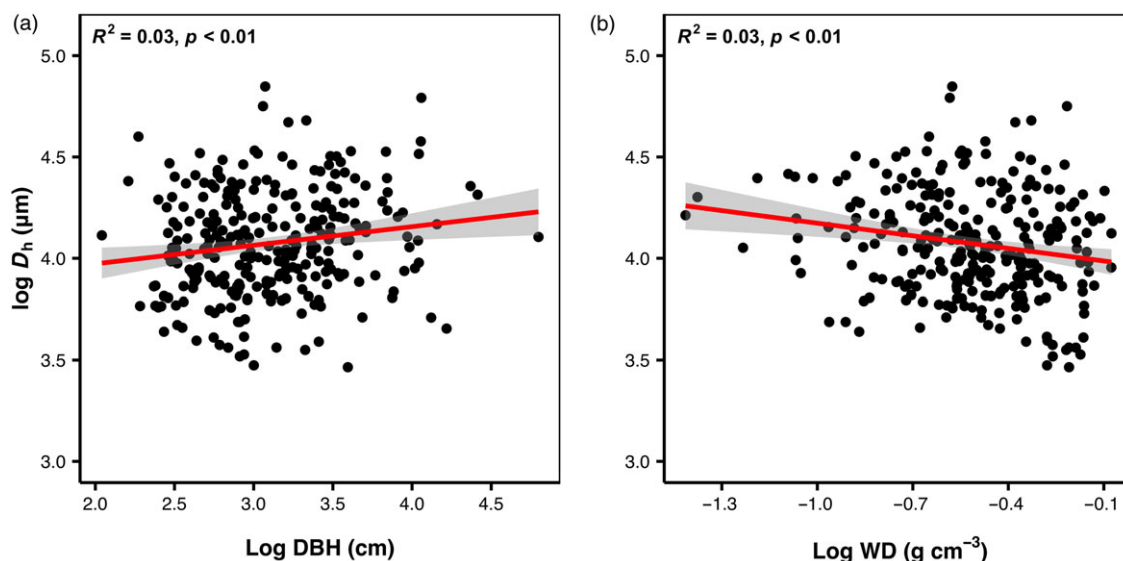
Figure 4. Diameter at breast height (a) and wood density (b) in relationship to the hydraulically-weighted vessel diameter of twigs across a wide range of tropical tree species.

Across species differing in height, we found several different vessel diameter distributions (Fig. 5). For example, the wood of *Dichapetalum gelonioides* (Roxb) Engl – a rather small species reaching 14 m height in our sample – is characterized by small vessels (10 – 40 µm in diameter), while *Syzygium acuminatissimum* (Blume) DC (21 m height) had a wider range of different vessel sizes and overall larger vessels (20–80 µm). In contrast, *Mezzettia parviflora* (Becc), which reaches different heights with *S. acuminatissimum and D. gelonioides* (46 m height), showed a different pattern than the two previous species by having vessel diameters ranging from 80 to 90 µm up to >100 µm.

4. Discussion

In our study across 279 lowland tropical tree species, we found a significant increase in hydraulically weighted vessel diameter (D_h) and potential hydraulic conductivity (K_p) with tree height. Because of the close relationship between tree height and the DBH, the latter was likewise closely related to D_h. Besides the well-described pattern of basipetal conduit widening from the apex towards the stem base in plants of all sizes and genera (Olson *et al.* 2021), the frequently observed phenomenon that tall trees show relatively larger vessels in their terminal twigs (cf. Kotowska *et al.* 2015, Liu *et al.* 2019, Olson *et al.* 2014, 2021, Schuldt *et al.* 2013, Zach *et al.* 2010) has not yet been elucidated. Although there are good arguments to expect conduit diameter at the same twig position to stagnate or even decline with increasing height, it is important to consider what organizational level has been analyzed. Our results are supportive for the assumption that the terminal twig anatomy is predetermined by the water demand a given species will reach at maturity, which explains why the grouped data according to the reported maximum tree height of a given species in the region revealed the closest relationship with D_h. This would imply a relatively close genetic control of initial vessel sizes of tree species when corrected for tree size and sampling position; with vessel diameters and potential conductivities of twigs showing much less variability within provenances and within species than other physiological and morphological traits associated with hydraulic functioning such as turgor loss point, $\delta^{13}C$, 50% of loss of hydraulic conductivity, and leaf morphological traits (Schreiber *et al.* 2011;

Hajek *et al.* 2016) and the expression of traits associated with hydraulic safety to be genetically controlled (Pritzkow *et al.* 2020). Across species, on the one hand, the terminal twig anatomy thus may reflect the growth potential and ecological niche (understory versus overstory or emergent) of a given species.

In the stem wood on the other hand, two gradients simultaneously affect vascular differentiation, namely the radial cambial age gradient that most likely can be attributed to different concentrations in plant hormones such as auxin (Hacke *et al.* 2017) and the vertical cell turgor gradient (cf. Li *et al.* 2019). In similar-sized branches with equal distance to the tip, only the vertical cell turgor gradient affects the vascular differentiation (Lockhart 1965, Woodruff *et al.* 2004, 2008). Within the canopy of five tall European beech trees, for example, Gottschall *et al.* (2019) observed a linear decline in vessel diameter in similar-sized branches from 17.3 ± 0.3 µm in 20 m height to 15.5 ± 0.3 µm 40 m height, i.e. by 11% only. In trees of the same species, the xylem anatomy of terminal twigs should therefore be more or less comparable as described above, because basipetal path length is the main driver and the most influential factor affecting xylem vessel diameter variation (Fajardo *et al.* 2020, Olson *et al.* 2014). However, studies currently show contrasted results, and it seems that vascular differentiation could also result from adaptive causes rather than non-adaptive ones such as vertical cell turgor gradient (Olson *et al.*, 2021).

A classic principle of plant hydraulic architecture postulates that the wood of trees growing in wet environments is composed of wider xylem conduits than the wood of trees from dry environments (Baas 1973, Carlquist 1977, Chenlemuge *et al.* 2015, Fajardo *et al.* 2020, Martinez-Cabrera *et al.* 2009, Pfautsch 2016, Schuldt *et al.* 2016). Only recently, however, it has been shown that water limitation does not directly translate into smaller xylem vessels, but that drought-exposure results in reduced growth and height and thus flow-path length from the stem base towards the distal twigs (Olson *et al.* 2014, 2018, 2020, 2021, Rosell *et al.* 2017). The tree species in this study evolved in humid tropical environments with precipitation rates beyond 2,000 mm yr^{-1} and do normally not face frequent drought stress, which can decrease water transport efficiency and might lower potential hydraulic conductivity of the xylem vessels. As an efficient and highly conductive xylem is
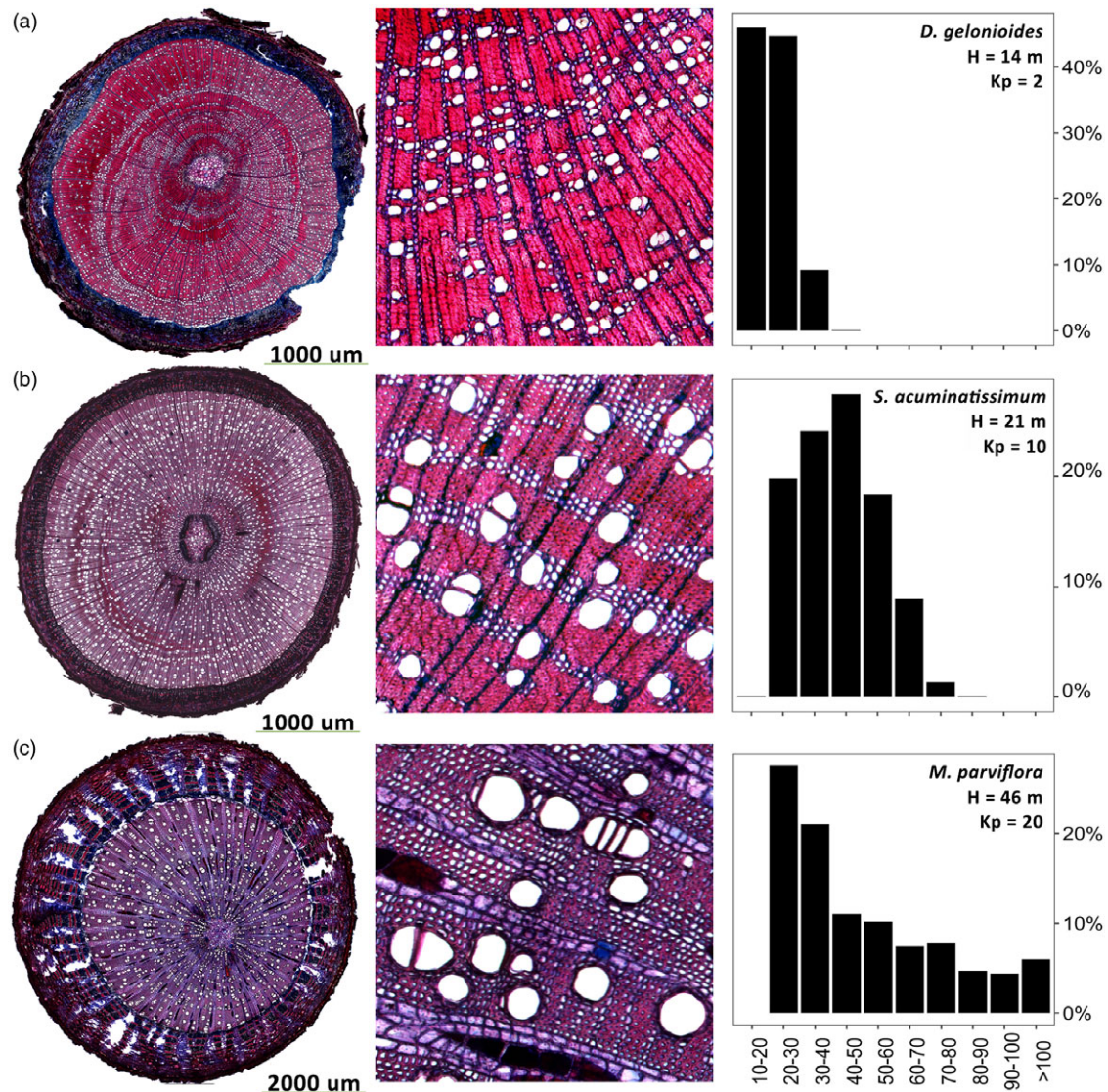
Figure 5. Vessel anatomy and frequency of three tropical tree species differing in their vascular architecture. Shown are three representatives for species with relatively small (*Dichapetalum gelonioides* (a)), medium (*Syzygium acuminatissimum* (b)), and large (*Mezzetia parviflora* (c)) vessel diameters.

indeed a perquisite for high sap flux densities in these trees (Kotowska *et al.* 2021) in response to a vertical gradient in evaporative demand within the stand (Schuldt *et al.* 2013), it seems beneficial for tall-growing overstory tree species to produce a highly efficient xylem that enables high transpiration rates during the diurnal peak in evaporative demand. Our results are in line with another tropical study (Zach *et al.* 2010) and a global meta-analysis (Liu *et al.* 2019).

Because of controversial reports in the literature, we further tested whether the terminal twig anatomy was related to WD. We assume that WD is indicative of twig wood density because this wood trait does not vary greatly along the flow path in tropical trees (Schuldt *et al.* 2013). In general, fast-growing species tend to have less compact wood than slow-growing species, which often is associated with a higher hydraulic efficiency (Enquist *et al.* 1999, King *et al.* 2006, Muller-Landau 2004, Poorter *et al.* 2008, 2010), but lower mechanical strength (Fan *et al.* 2017). While several studies have shown that wood density is related to xylem anatomy as well as hydraulic properties (Hoeber *et al.* 2014, McCulloh *et al.* 2011, Roque & Tomazelo-Filho 2007), others could not confirm

these findings (Kotowska *et al.* 2015, Martinez-Cabrera *et al.* 2009, Poorter *et al.* 2010, Russo *et al.* 2010). It was speculated that a given drought-stress exposure is needed to observe such a relationship (Schuldt *et al.* 2013). Although the tree species of our study are not exposed to frequent edaphic or climatic aridity, we likewise observed a weak but significant negative relationship between D_h and wood density in contrast to the assumption by Schuldt *et al.* (2013). The reason for this remains speculative because vessel diameter variation is only one component that affects differences in wood density across species due to its effect on the lumen-to-sapwood area ratio, and thus the space available for carbon storage. In addition, fibres and parenchymatic tissue strongly influence wood density variation (Ziemińska *et al.* 2013, 2015).

5. Conclusions

The purpose of the current study was to analyze the effect of tree height on xylem anatomical traits of terminal twigs from fully grown individuals of 279 tropical lowland tree species. We show

that hydraulically weighted vessel diameter (D_h) and potential hydraulic conductivity (K_p) increase with tree height across a wide range of species and values were largest in the species reaching the upper canopy. Evidence from this study points towards a differentiation of hydraulic strategies between functional groups with tree species reaching upper canopy or emergent position in tropical forests having distinct vascular anatomical adaptions i.e. larger vessel diameter in their terminal wood anatomy than tree species occurring in the understorey. The resulting highly conductive xylem allows to maximize for higher sap flux rates per cross sectional area and meet the water demand of the sun-exposed canopy experiencing pronounced fluctuations of vapor pressure deficits. To determine whether these observations are indeed based on a conservative trait expression under mainly genetic control, we emphasize the priorities of follow-up studies. These should focus on incorporating data on within-species variability, assembling one the one hand data on vascular anatomy along the whole flow path starting from leaf veins, to leaf petioles and following down to the stem while correcting for tree height and distance to leaf tip, and on the other hand, comparing whether various ontogenetic stages such as seedings, sapling and adult trees of tree species from different functional groups already show anatomical perquisite for their future ecological niche. Furthermore, incorporating phylogenetic information and – if feasible – using progeny trials will allow to determine the proportion of variance in vessel anatomy explained by phenotypic plasticity versus genetic control.

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