

# Wood traits related to size and life history of trees in a Panamanian rainforest

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## Introduction

The main functions of wood – mechanical support, water and nutrient transport, and storage – are reflected in its anatomy and in emergent functional traits. Vessels enable long-distance axial transport, lignified cell walls and particularly fibres add strength, and living parenchyma cells provide radial transport and storage. The relative allocation of wood to these tissues reflects the relative importance of the corresponding functions for particular species, and, because a higher proportion of one cell type will mean a lower proportion of another type, there appear to be potential trade-offs. Here, we will focus on relationships and potential trade-offs among vessel properties, hydraulic conductivity, wood density (WD) and tree demography and life history.

Wood hydraulic conductivity (Kh) depends on vessel lumen area and vessel density. To increase hydraulic conductivity, plants can either dedicate a larger fraction of the cross-sectional area (the vessel lumen fraction *F*) to water transport, or make fewer but larger vessels. According to the Hagen–Poiseuille law, Kh scales with the square of the area of individual vessels and with vessel number (Zimmermann, 1983); thus, increasing vessel size will have a stronger effect on Kh than increasing vessel number with constant *F*, and trees with large vessels could reduce *F* and dedicate greater cross-sectional area to mechanical strength or storage without compromising Kh. However, a worldwide comparison

## Summary

- Wood structure differs widely among tree species and species with faster growth, higher mortality and larger maximum size have been reported to have fewer but larger vessels and higher hydraulic conductivity (Kh). However, previous studies compiled data from various sources, often failed to control tree size and rarely controlled variation in other traits.
- We measured wood density, tree size and vessel traits for 325 species from a wet forest in Panama, and compared wood and leaf traits to demographic traits using species-level data and phylogenetically independent contrasts.
- Wood traits showed strong phylogenetic signal whereas pairwise relationships between traits were mostly phylogenetically independent. Trees with larger vessels had a lower fraction of the cross-sectional area occupied by vessel lumina, suggesting that the hydraulic efficiency of large vessels permits trees to dedicate a larger proportion of the wood to functions other than water transport.
- Vessel traits were more strongly correlated with the size of individual trees than with maximal size of a species. When individual tree size was included in models, Kh scaled positively with maximal size and was the best predictor for both diameter and biomass growth rates, but was unrelated to mortality.

of wood anatomy found *F* to be independent of vessel size (Zanne *et al.*, 2010).

Mechanical strength and stiffness are strongly related to WD (Niklas, 1992). Because vessel lumina dedicated to water transport cannot contribute to WD, there might also be a trade-off between the ability of a stem to supply leaves with water and its mechanical strength. A negative correlation between WD and *F* was found in some studies (Preston *et al.*, 2006; Jacobsen *et al.*, 2007), but not in others (Martínez-Cabrera *et al.*, 2011) nor in a large compilation of published data (Zanne *et al.*, 2010). A negative WD–*F* relationship could reflect a trade-off, but could also appear if WD and water transport capacity were both related to a third factor, such as variation in life-history strategies.

WD also scales negatively with species-specific growth and mortality rates (Muller-Landau, 2004; Poorter *et al.*, 2008, 2010; Kraft *et al.*, 2010; Wright *et al.*, 2010), reflecting the strategy of fast-growing and short-lived species to invest in light, poorly defended wood rather than mechanical strength, drought resistance, and long-term defence. Kh and vessel lumen area scale positively with growth because high rates of water transport are necessary to maintain stomatal conductance and photosynthesis in fast-growing trees (Poorter *et al.*, 2010). Kh and vessel lumen area also scale positively with maximum height of adult trees, presumably due to the importance of transporting water efficiently to great height (Poorter *et al.*, 2010). Rainforest trees with a

greater maximum height have higher rates of photosynthesis, as saplings and adult trees, than do species that do not grow tall (Thomas & Bazzaz, 1999) and likely also have higher water use. By contrast, the main advantage of small vessels is thought to be redundancy in water transport and increased resistance against embolism (Hacke *et al.*, 2009). Embolism resistance is correlated with WD (Hacke *et al.*, 2001) although this is not seen in all studies (Jacobsen *et al.*, 2008; Meinzer *et al.*, 2008b).

Although wood traits are important to support leaves, leaf traits such as nitrogen concentration ( $N_{\text{leaf}}$ ) and leaf mass per area (LMA) are directly related to photosynthetic capacity at the leaf level (Wright *et al.*, 2004) and, thus, with growth rates (Poorter & Bongers, 2006). Likewise, height is closely correlated with growth rates because taller trees intercept more light and potentially have higher rates of photosynthesis. In contrast to  $N_{\text{leaf}}$ , LMA and maximum size, WD does not enable higher rates of photosynthesis. Many studies have studied relationships between growth rates and functional traits and several have evaluated the effect of multiple traits in models (Poorter *et al.*, 2008; Wright *et al.*, 2010; Rüger *et al.*, 2012; Visser *et al.*, 2016), but to our knowledge no study has integrated hydraulic conductivity in combination with other traits to explain growth rates in a forest community.

Relationships between traits and growth rates depend on the measure of growth. This is particularly true for WD because WD is used in the calculation of biomass growth rates. Despite strong interest in biomass growth and the carbon balance of forests, most studies evaluate relationships between functional traits and diameter growth (e.g. Poorter *et al.*, 2008, 2010; Martínez-Vilalta *et al.*, 2010; Russo *et al.*, 2010; Wright *et al.*, 2010; Hérault *et al.*, 2011; Iida *et al.*, 2013). WD and diameter growth rates are inversely related, but relationships between WD and biomass growth rates are less consistent. Biomass growth is negatively related to WD and positively related to hydraulic conductivity for a semi-dry forest (Hoerber *et al.*, 2014). Biomass growth is unrelated to WD in small trees in a humid tropical forest, but large trees with high WD have higher biomass growth than low WD trees (Rüger *et al.*, 2012). The familiar inverse relationship between WD and diameter growth rates might thus reflect preferential allocation to diameter growth vs investment in resistant wood and be unrelated to the capacity to acquire resources in the first place.

Wood traits are heritable and are subject to evolutionary modification (Carlquist, 2012). Because related species tend to be similar, wood traits may enable some lineages to grow in environments where others are not found (Zanne *et al.*, 2014) and exploit niches such as early successional forests (Letcher *et al.*, 2015). WD, vessel density and vessel area are phylogenetically conserved, but the relationship between vessel area and density has phylogenetically independent origins (Preston *et al.*, 2006). This means that vessel area and density evolved in a coordinated way, presumably because optimal wood function constrains the possible combinations of vessel areas and densities.

Wood functional traits often scale with tree size, which is evident from radial variation of wood properties from the stem centre to the cambium (reviewed in Lachenbruch *et al.*, 2011). WD scales with stem diameter in some species but not in others, often

increasing but less commonly decreasing from pith to bark (Wiemann & Williamson, 1988; Nock *et al.*, 2009; Hietz *et al.*, 2013). Resistance in a conducting pipe increases with pipe length, and vessel size scales with stem length and size in self-supporting plants (Olson *et al.*, 2014). Plant size is also related to physiological traits, including photosynthesis and water relationships (de Soyza *et al.*, 1996; Midgley, 2003), but most studies of interspecific variation in traits do not control plant size. For this reason, it is often unclear whether correlations of demographic traits with wood traits and differences in wood traits among species are due to interspecific variation or to variation among individual plants of different sizes.

In order to better understand structural adaptations of wood and its importance for tree function, we analysed wood density and anatomy for 325 species from a tropical moist forest on Barro Colorado Island (BCI), Panama. Combined with a long-term study of forest dynamics, from which demographic data for many of the study species are available, this represents the most extensive dataset linking wood functional traits to demographic traits (growth, mortality and maximum tree size) for a tree community. Combining these datasets, we address the following questions. Given that vessel lumina conduct water, but do not contribute to WD and mechanical strength, do trees face a trade-off between WD and the cross-sectional area dedicated to water transport (F) – and thus Kh? How strongly are different wood traits phylogenetically conserved and do correlations between traits have phylogenetically independent origins or result from evolutionary relationships among species (Felsenstein, 1985)? Wood traits are known to change as a tree grows and measurements obtained from outer wood (sapwood) will thus differ depending on the size of the sampled tree. How are apparent relationships between wood traits and demographic traits affected when size is controlled? Which traits most affect growth and mortality? Productive leaves and the capacity to supply the leaves with water drive high growth rates. We predict that leaf traits, vessel diameter and Kh will be related to tree growth rates and that WD will be related to diameter growth, but not to biomass growth.

## Materials and Methods

### Sampling

A 50-ha forest plot was established in a primary tropical moist forest on Barro Colorado Island (BCI), Panama in 1982 and remeasured in 1985 and every 5 yr since (Condit *et al.*, 2006). At BCI, the temperature averages 27.4°C, and annual rainfall averages c. 2600 mm with a four month dry season (< 100 mm rainfall per month). Because tree coring is prohibited on BCI, wood samples were collected nearby in similar tall (> 20 m), closed canopy, moist forests. In contrast to the primary forest on BCI, these were late secondary forests, mostly from the second half of the 19<sup>th</sup> Century (and estimated to be 130–150 yr old), but a few stands from after the time of the Panama Canal construction (1914) or after WWII (1945). Generally, five mature trees per species were cored at breast height with standard 5-mm increment borers and the diameter at breast height (DBH, ranging from 6 to 207 cm)

and the GPS coordinates were recorded. We use  $DBH_s$  to refer to the diameter of the cored tree and  $DBH_{max}$  for the maximum diameter of a species (see later). Cores were split into 5-cm segments and the wood density (WD,  $g\ cm^{-3}$ ) of all samples was determined by the water displacement method as mass after drying at  $100^\circ C$  divided by green volume (Wright *et al.*, 2010; Hietz *et al.*, 2013). We randomly choose one of the five cored trees per species for wood anatomical analysis (see later).

Leaves were sampled from the uppermost branches of the six tallest trees of each species in the 50-ha plot and used to measure leaf area ( $cm^2$ ), leaf mass per area (LMA;  $g\ m^{-2}$ ) and leaf nitrogen content ( $N_{leaf}$ ; %) (Wright *et al.*, 2010).

### Anatomical analysis

We analysed the outermost segment – that is, wood within 5 cm from the cambium and mostly within 1 cm – from one individual for each of 325 tree species (species shown in Supporting Information Fig. S1). For statistical comparisons between wood anatomy and WD, we used the WD of the sample ( $WD_s$ ) used for the anatomical measurements rather than mean density of the species. However, for analyses relating demographic traits and functional traits, we used the mean WD ( $WD_m$ ) of the five sampled trees, with  $WD_s = 0.068 + 0.89 \times WD_m$ ,  $r^2 = 0.802$ . To calculate  $WD_m$ , each segment was weighted by the area of the annulus it represented, assuming a cylindrical trunk, so that  $WD_m$  reflects the density of a stem disk in which the small volume of wood in the centre contributes less than the larger volume of wood close to the bark.

We made 20–30- $\mu m$  transverse sections with a sliding microtome, stained with methylene blue and embedded in Euparal (Carl Roth, Karlsruhe, Germany). Several photos were taken from each section with a microscope (DM4000M; Leica Microsystems, Wetzlar, Germany) equipped with a digital frame grabber. The lumen areas of vessels (hereafter called vessel area) were colour-coded manually using the ‘flood fill’ feature of PHOTOSHOP (CS3; Adobe Systems, San José, CA, USA). The area, maximum width and the width perpendicular to the maximum width of each vessel, as well as the total area of the section analysed, were then measured automatically with SIGMA SCAN Pro (Systat Software Inc., Chicago, IL, USA). The area of the section analysed ranged between 1.7 and  $140\ mm^2$  (mean 21) and included between 26 and 1362 (mean 240) vessels.

### Data analysis

For each species, we calculated individual vessel area (VA,  $mm^2$ ); vessel density (VD, vessels per  $mm^2$ ) and F, which is the proportion of the section occupied by vessel lumina. Wood hydraulic conductivity (Kh,  $kg\ m\ MPa^{-1}\ s^{-1}$ ) was calculated according to the Hagen–Poiseuille law where  $Kh = \rho w / (128\ \eta)\ VD\ Dh^4\ 10^6$ , where  $\rho w$  is the density of water at  $20^\circ C$  ( $998.2\ kg\ m^{-3}$ ) and  $\eta$  is the viscosity of water at  $20^\circ C$  ( $1.002 \times 10^{-9}\ MPa\ s$ ). Dh, the mean hydraulically weighted vessel diameter, was calculated as  $Dh = (\sum D^4/n)^{1/4}$ , where D is the average of the major and minor axis for each vessel cross-section (in mm) and n is the total number

of vessels measured (Tyree & Zimmermann, 2002). The calculated Kh based on the Hagen–Poiseuille law is substantially higher than true conductivity as it ignores resistance of water flowing through the vessel walls. However, vessel walls contribute a relatively constant 56% ( $\pm 2\%$ ) to total resistance in conduits (Sperry *et al.*, 2006), thus calculated Kh appears to be a good proxy for true conductivity. Because vessels are generally elliptical and often circular, VA and  $D^2$  are strongly correlated ( $r^2 = 0.99$ ).

We analysed only one wood sample per species from a location different from the long-term monitoring plot. To assess the potential effect of within-species variation, we measured vessels in three individuals for 18 species to calculate within and among species variance, and used a Mantel test (Legendre & Fortin, 1989) to evaluate the potential effect of spatial variation (see Notes S1 for details).

Information on maximum tree size and demographic parameters were obtained from census data measured in the 50-ha plot on BCI in 1982, 1985, 1990, 1995, 2000 and 2005 (Wright *et al.*, 2010). We calculated diameter growth (DGR) and mortality (M) rates for trees  $\geq 100\ mm$  DBH because wood samples were from the outer 5 cm of the cores and thus represent larger trees, and because DGR as well as wood structure can change rapidly in small trees. Individual-level DGR equals  $100 \times \log_e(DBH_f/DBH_i)/\Delta t$ , where  $\Delta t$  is the time in years between measurements. The subscripts f and i refer to final and initial values, respectively. Population-level mortality rates equal  $100 \times (1 - (N_f/N_i))$ , where  $N_i$  is the number of individuals present initially and  $N_f$  is the number of survivors (Wright *et al.*, 2010). Relationships with growth rates and M were evaluated only for species with at least 50 observations. Maximum height ( $H_{max}$ ) and maximum DBH ( $DBH_{max}$ ) are the means of the six largest (by DBH) individuals of each species in the BCI 50-ha plot in 2007 (Wright *et al.*, 2010).

Relative DGR is a useful measure to compare changes in size and growth trajectories between species, but not to assess differences in biomass investment because the same volume increment requires greater biomass for high-density than for low-density wood. To calculate biomass growth rates, we estimated the above-ground biomass (AGB) of trees using a general allometric model for tropical wet forest trees (Chave *et al.*, 2014:  $AGB = \exp(-1.803 - 0.976 \times E + 0.976 \times \log(WD) + 2.673 \times \log(DBH) - 0.0299 \times \log(DBH)^2)$  with DBH in cm and E a parameter depending on climate ( $E = 0.07072$  for BCI). Starting with a DBH of 100 mm in year 0, DBH will be  $100 \times e^{DGR/100}$  in year 1. Using DGR for trees  $\geq 100\ mm$  DBH, total biomass growth rate (BGR) in 1 year is calculated as the difference in AGB between trees with diameters of 100 mm and  $100 \times e^{DGR/100}\ mm$ .

We calculated ordinary least-square regressions to describe relationships between two variables, and used Fisher’s  $r$ -to- $z$  transformation to determine whether correlation coefficients ( $r$ ) differed significantly between wood traits and  $DBH_{max}$  vs  $DBH_s$ .

We performed multiple regression analyses to evaluate the relationships between demographic traits (DGR, BGR and M) and wood and leaf traits (LMA,  $N_{leaf}$ , leaf area, Kh and mean  $WD_m$ ). We performed a second multiple regression analysis to evaluate relationships between  $H_{max}$  and Kh, and mean  $WD_m$ . Leaves sampled

from the uppermost branches of small species were shaded, those of large trees were sun-exposed and leaf traits vary with light intensities, and, for these reasons, leaf traits were not used to explain  $H_{\max}$ . Because Kh was obtained from a single individual and wood traits are known to change with diameter, the starting model included an interaction term  $\text{Kh} \times \text{DBH}_s$ . We used backward stepwise multiple regression analyses, eliminating insignificant variables from the model until only significant variables remained. The variance inflation factor, a measure of collinearity, was  $< 2$  in the most complex models, indicating that collinearity between variables was not a problem. All variables except WD and  $H_{\max}$  were log-transformed to meet assumptions of normality.

We calculated one principal component analysis (PCA) to evaluate associations among wood traits and a second PCA to evaluate associations among wood traits, leaf traits,  $\text{DBH}_s$  and demographic traits (DGR, BGR, M). The second PCA excludes maximum tree size because the pairwise regression analyses showed that  $\text{DBH}_s$  was a better predictor than  $\text{DBH}_{\max}$ . Because vessel traits are strongly related, we used Kh as the only trait for vessels in the second PCA to prevent it from being skewed by an obvious trade-off between VA and VD. For the PCAs, data were mean-centred and scaled to have unit variance. Because the species for which wood samples were available were not all represented in the 50-ha plot and demographic parameters were used only for species with  $> 49$  records, the second PCA was calculated with 98 species for which all variables were available.

We quantified phylogenetic signal for wood traits with Pagel's lambda (Pagel, 1999) using the 'PHYLOSIG' function in the R package 'PHYTOOLS'. We tested whether wood traits differed among 12 families with a minimum of ten species each with analysis of variance. We tested whether the slopes of the correlation between VA and VD differed among families and whether the regression slopes from our dataset differed from a large global dataset (Zanne *et al.*, 2010) with standardized major axis (sma) tests using the R package 'SMATR'.

In order to test if correlations resulted from phylogenetic relatedness, we also calculated pairwise correlations using phylogenetically independent contrasts (PICs; Felsenstein, 1985). We constructed a phylogenetic tree using PHYLOMATIC (Webb *et al.*, 2008; <http://www.phylodiversity.net/phylocom/>) based on the APG3-derived megatree. We did not use the DNA-based phylogeny of 300 BCI trees (Kress *et al.*, 2009) because this covers only about half of our species. We used estimated ages of nodes (Wikström *et al.*, 2001) to date all other nodes by dividing branch lengths evenly between the dated nodes. Polytomies in the Phylomatic tree were resolved with the R function MULTI2DI. PICs were calculated with the R package PICANTE with PIC regressions forced through the origin. Statistics were calculated with R v.3.2.1 (R Development Core Team, 2011).

## Results

### Relationships among wood traits

Wood anatomy and calculated Kh varied substantially among species (Table 1). Within-species variation of wood traits was

about an order of magnitude lower than among-species variation. Spatial effects were insignificant for VA, DV and Kh (Mantel test,  $P > 0.9$ ) and significant ( $P = 0.04$ ) but low ( $r^2 = 0.0027$ ) for WD (see Notes S1). This may be relevant because wood traits were not obtained from the site with the permanent plot, where life-history traits were obtained from.

$\text{WD}_s$  was positively correlated with VD and negatively correlated with VA and Kh (Table 2).  $\text{WD}_s$  was not correlated with lumen fraction (F). Kh was strongly, positively correlated with VA ( $r^2 = 0.76$ ), positively correlated with F ( $r^2 = 0.18$ ), and negatively correlated with VD ( $r^2 = 0.31$ ). F increased with VD ( $r^2 = 0.27$ ), but was unrelated to VA ( $r^2 = 0.00$ ) in spite of the very strong VD–VA relationship ( $r^2 = 0.77$ , Fig. 1). The slope of the relationship between VA and VD was  $-0.85$  and significantly different from  $-1$  ( $P < 10^{-8}$ ). The VA–VD slope did not differ between families in our dataset ( $P = 0.656$ ) but did differ significantly ( $P < 10^{-5}$ ) between our dataset and a published global dataset (Fig. 1; Zanne *et al.*, 2010).

The PCA with all wood traits showed most traits except F scaling predominantly on the first axis, with  $\text{WD}_s$  and VD scaling in one direction, and Kh,  $\text{DBH}_s$ , Dh and VA in the other direction. Only F scaled strictly on the second axis, orthogonally to VA, Dh and  $\text{WD}_s$  (Fig. 2).

### Phylogenetic relationships

Phylogenetic signal (lambda) was high for VA (0.75), VD (0.79) and  $\text{WD}_m$  (0.77), but substantially lower for F (0.55) and Kh (0.50) even though both are derived from VA and VD. Family had a highly significant effect on all wood traits in one-way ANOVAs ( $P < 0.001$ ).

PIC correlations were mostly similar to species-wise correlations (Table 2), which suggests that the relationships found were mostly not driven by phylogenetic relatedness.

### Relationships with individual tree size and species-level maximum tree size

VA, VD and Kh were more strongly correlated with the DBH of the individual trees sampled than with the maximum DBH

**Table 1** Mean and range of wood anatomical traits measured for 325 trees from a Panamanian wet forest

|   | Max/<br>Min | Max   | Min    | Mean  | SD    |
|---|-------------|-------|--------|-------|-------|
| $\text{WD}_s$ ( $\text{g cm}^{-3}$ )                    | 4.6         | 0.89  | 0.19   | 0.58  | 0.142 |
| $\text{WD}_m$ ( $\text{g cm}^{-3}$ )                    | 5.2         | 0.87  | 0.17   | 0.57  | 0.143 |
| VA ( $\text{mm}^2$ )                                    | 105         | 0.057 | 0.0005 | 0.010 | 0.009 |
| VD (vessels $\text{mm}^{-2}$ )                          | 262         | 274   | 1.0    | 19.5  | 28.5  |
| F (%)   | 26.8        | 30.5  | 1.1    | 8.4   | 4.5   |
| Dh (mm)   | 10.6        | 0.31  | 0.029  | 0.12  | 0.052 |
| Kh ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) | 222         | 601   | 2.7    | 55.8  | 72.7  |

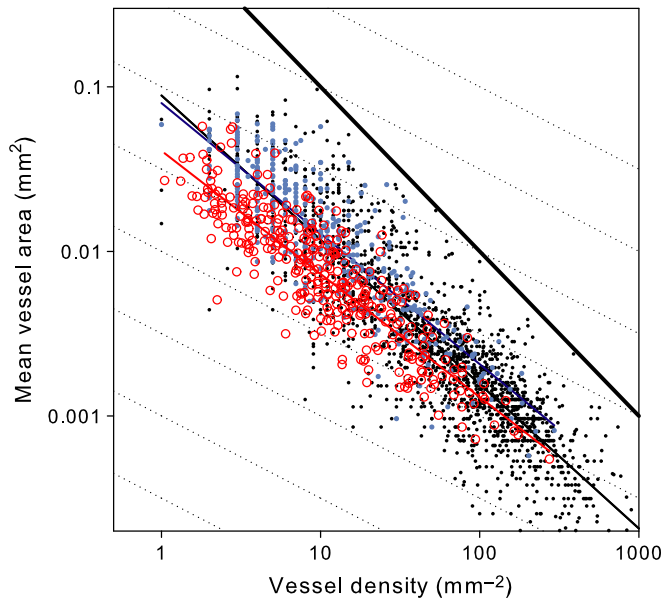
$\text{WD}_s$ , wood density of the sample used for anatomy;  $\text{WD}_m$ , mean wood density per species; VA, individual vessel area; VD, vessel density; F, vessel lumen fraction; Dh, hydraulically weighted vessel diameter; Kh, calculated hydraulic conductivity.



**Table 2** Pearson correlations between traits of 325 tree species from a Panamanian wet forest

|                  | WD            | VA            | VD            | F            | Dh            | Kh            | H <sub>max</sub> | DGR           | BGR          | M             |
|------------------|---------------|---------------|---------------|--------------|---------------|---------------|------------------|---------------|--------------|---------------|
| WD               |               | <b>-0.334</b> | <b>0.241</b>  | -0.091       | <b>-0.339</b> | <b>-0.353</b> | <b>-0.183</b>    | <b>-0.369</b> | 0.144        | <b>-0.345</b> |
| VA               | <b>-0.278</b> |               | <b>-0.878</b> | -0.052       | <b>0.997</b>  | <b>0.860</b>  | <b>0.380</b>     | <b>0.374</b>  | 0.109        | 0.142         |
| VD               | <b>0.206</b>  | <b>-0.819</b> |               | <b>0.524</b> | <b>-0.879</b> | <b>-0.519</b> | <b>-0.332</b>    | -0.232        | -0.015       | -0.125        |
| F                | -0.094        | <b>0.207</b>  | <b>0.392</b>  |              | -0.060        | <b>0.448</b>  | 0.007            | 0.214         | 0.173        | 0.006         |
| Dh               | <b>-0.285</b> | <b>0.996</b>  | <b>-0.821</b> | <b>0.198</b> |               | <b>0.864</b>  | <b>0.379</b>     | <b>0.373</b>  | 0.106        | 0.151         |
| Kh               | <b>-0.273</b> | <b>0.872</b>  | <b>-0.445</b> | <b>0.640</b> | <b>0.877</b>  |               | <b>0.342</b>     | <b>0.423</b>  | 0.171        | 0.141         |
| H <sub>max</sub> | -0.051        | <b>0.253</b>  | -0.193        | 0.087        | <b>0.248</b>  | <b>0.228</b>  |                  | <b>0.324</b>  | 0.231        | -0.220        |
| DGR              | <b>-0.374</b> | <b>0.361</b>  | <b>-0.249</b> | 0.131        | <b>0.355</b>  | <b>0.332</b>  | <b>0.296</b>     |               | <b>0.861</b> | <b>0.298</b>  |
| BGR              | 0.068         | 0.157         | -0.110        | 0.056        | 0.149         | 0.135         | <b>0.276</b>     | <b>0.894</b>  |              | 0.165         |
| M                | <b>-0.257</b> | -0.037        | 0.036         | 0.001        | -0.025        | -0.009        | <b>-0.242</b>    | 0.213         | 0.122        |               |

Species-wise correlations are shown above and phylogenetically independent contrast (PIC) correlations below the diagonal. Significance levels: italicized, <0.05; bold, <0.01; italicized and bold <0.001. Because not all traits were available for the same number of trees,  $n = 325$  for correlations of wood traits,  $n = 182$  for correlations with H<sub>max</sub>,  $n = 119$  for relative diameter growth rate (DGR) and relative biomass growth rates (BGR) and  $n = 127$  for mortality (M). WD, wood density (the density of the 5-cm core sample used for wood analysis for correlation with wood traits (VA to Kh), which were obtained from the same sample, but the mean WD of five trees per species for correlations with life-history traits (H<sub>max</sub> to M)); VA, individual vessel area; VD, vessel density; F, vessel lumen fraction; Dh, hydraulically weighted diameter; Kh, calculated hydraulic conductivity; DGR, relative diameter growth rate; BGR, relative biomass growth rates; M, mortality, (see the Materials and Methods section for details). All data except WD and H<sub>max</sub> were log-transformed.

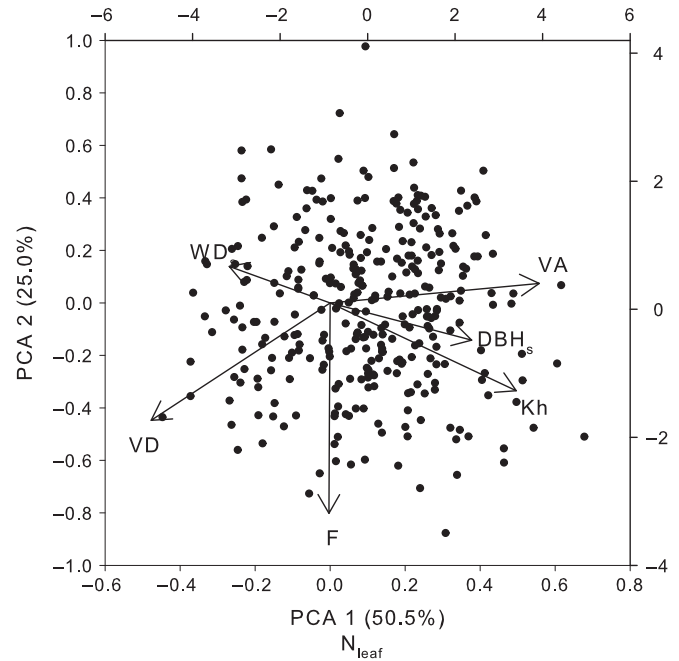


**Fig. 1** Relationship between vessel density and mean vessel area for 325 species from a wet forest in Panama (red circles), for 2230 species in a global dataset (small black and blue symbols, Zanne *et al.*, 2010) and for 409 tropical species from the global dataset (blue symbols). The red, black and blue lines are the linear regression lines for the respective datasets. The thick black line is the theoretical limit where lumen fraction  $F = 1$  and the thin dotted lines are isolines representing combinations of vessel density and size that result in the same calculated hydraulic conductivity (Kh).

measured in the species (Fig. 3). For species-wise comparisons, the differences between correlation coefficients with DBH<sub>max</sub> and DBH<sub>s</sub> were significant ( $P < 0.05$ ) for VA, Dh and Kh. For PICs, differences were significant ( $P < 0.01$ ) for VA and Kh, and marginally significant ( $P = 0.07$ ) for VD.

#### Relationship between functional and demographic traits

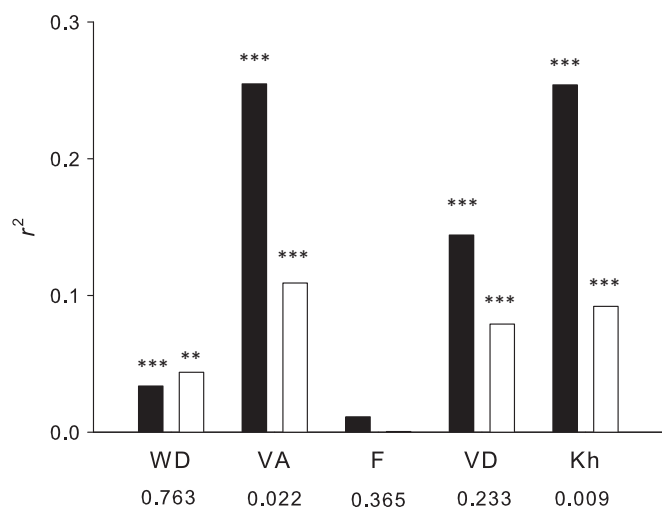
In multiple regression models, diameter and biomass growth rates were significantly related to WD<sub>m</sub>, N<sub>leaf</sub> and Kh, with Kh



**Fig. 2** Principal component analysis (PCA) of wood traits for tree species from a Panamanian wet forest. DBH<sub>s</sub>, diameter at breast height of the sampled individual; Kh, calculated hydraulic conductivity; VD, vessel density; VA, mean area of individual vessels; Dh, hydraulically weighted vessel diameter; F, vessel lumen fraction; WD<sub>s</sub>, wood density of the sample used for anatomy. Values in parentheses in the axis labels are percentages explained by the first two components.

having the highest significance (Table 3). WD<sub>m</sub> was negatively related to DGR but positively to BGR. LMA and leaf area were not significantly related to growth rates. WD<sub>m</sub> was negatively related to M, and Kh and the interaction term (Kh × DBH<sub>s</sub>) explained significant variation in H<sub>max</sub>.

The first four axes in the PCA with wood, leaf and demographic traits as well as DBH<sub>s</sub> explained 30.6%, 23.7%, 14.1% and 9.8% of the variation, respectively. WD<sub>m</sub>, Kh and DBH<sub>s</sub>



**Fig. 3** Species-wise correlations ( $r^2$ ) between wood traits and either the diameter of the sampled tree (DBH<sub>s</sub>; closed bars) or the maximum diameter of a species (DBH<sub>max</sub>; open bars). Asterisks indicate significant effects of DBH<sub>s</sub> or DBH<sub>max</sub> (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ). Numbers below the trait abbreviations on the x-axis are  $P$ -values testing if  $r^2$ -values for correlations with DBH<sub>s</sub> were significantly different from  $r^2$ -values with DBH<sub>max</sub>. See Fig. 2 for abbreviations.

had strong loadings on the first axis, and leaf traits had strong loadings on the second axis. DGR, BGR and M all scaled on the first and second axis, positively with Kh, DBH<sub>s</sub>, LA and N<sub>leaf</sub>, negatively with WD<sub>m</sub> and nearly orthogonally with LMA (Fig. 4).

## Discussion

Similar to previous studies (Chave *et al.*, 2009; Zanne *et al.*, 2010), we found large variation in wood structure (Table 1), which we hypothesized to be related to tree demographic traits. We evaluated hypotheses using a large dataset, obtained with a uniform methodology, from a single tropical forest with long demographic records. We first discuss correlations between wood

traits and a potential trade-off between mechanical support and hydraulic conductivity. We then ask if phylogeny constrains relationships between wood traits and growth strategies. Because the structure of newly produced wood often changes as the tree grows, and is consequently related to the size of a tree (Lachenbruch *et al.*, 2011), we discuss the importance of including individual tree size in interspecific analyses of wood function and finally ask which functional traits best explain tree life history.

### Do mechanical and hydraulic functions compete for available wood volume?

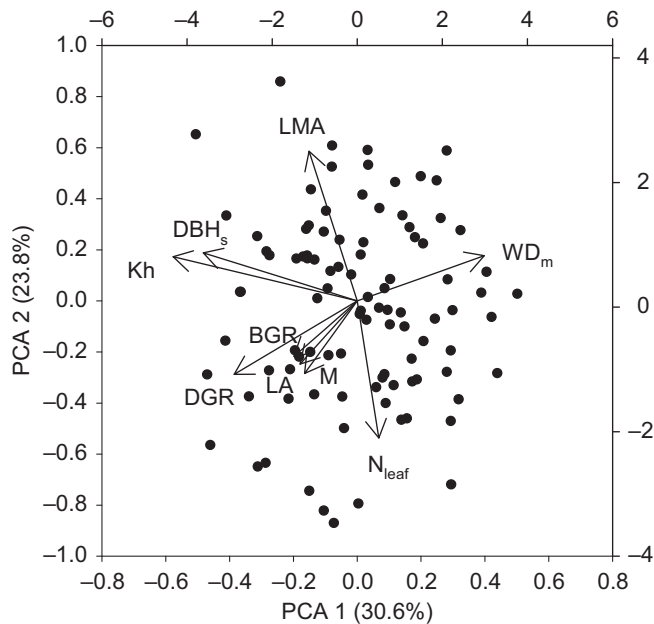
Although more vessels can transport more water, calculated hydraulic conductivity (Kh) and vessel density (VD) are negatively correlated because of the strong negative correlation between individual vessel area (VA) and VD (Fig. 1) and because Kh increases linearly with VD but with the square of VA. The negative correlation between sample wood density (WD<sub>s</sub>) and Kh ( $r = -0.353$ , Table 2) remained highly significant when tree size was included, which suggests a trade-off between water transport and WD and hence a trade-off between water transport and mechanical support, which increases with WD (Niklas, 1992); however, the relationship between WD<sub>s</sub> and vessel lumen fraction (F) (Table 2) was insignificant. Thus, water transport capacity does not appear to trade off with the cross-sectional area of wood available for mechanical strength. WD was also unrelated to vessel, fibre or parenchyma area for 42 tropical trees from Bolivia (Poorter *et al.*, 2010).

By contrast, a strong negative correlation ( $r = -0.56$ ) between WD<sub>s</sub> and F has been reported for chaparral, a Californian vegetation with Mediterranean climate (Preston *et al.*, 2006). Wood from chaparral might differ from rainforest wood because dry forest trees on average have higher wood densities than wet forest trees (Chave *et al.*, 2009), which means that a larger proportion of wood volume is occupied by cell walls. At the same time, F was also greater for chaparral shrubs than for tropical humid forest trees. Allocation to mechanical strength (wood density)

**Table 3** Multiple regression models of relationships between life-history traits and key functional traits

|                       | DGR      |        | BGR      |        | M        |         | H <sub>max</sub> |         |
|-----------------------|----------|--------|----------|--------|----------|---------|------------------|---------|
|                       | Estimate | $P$    | Estimate | $P$    | Estimate | $P$     | Estimate         | $P$     |
| Intercept             | 1.759    | < 1e-4 | 0.594    | 0.139  | 3.455    | < 1e-11 | 27.040           | < 1e-4  |
| WD <sub>m</sub>       | -0.728   | 0.038  | 1.136    | 0.002  | -1.648   | < 1e-5  | ns               |         |
| N <sub>leaf</sub>     | 0.380    | 0.023  | 0.392    | 0.023  | ns       |         | -                |         |
| Kh                    | 0.166    | 0.0004 | 0.165    | 0.0006 | ns       |         | 4.298            | < 1e-11 |
| Kh × DBH <sub>s</sub> | ns       |        | ns       |        | ns       |         | -0.690           | < 1e-10 |
| LMA                   | ns       |        | ns       |        | -0.372   | 0.049   | -                |         |
| Leaf area             | ns       |        | ns       |        | ns       |         | -                |         |
| $r^2$ adjusted        | 0.258    |        | 0.110    |        | 0.155    |         | 0.304            |         |
| df                    | 100      |        | 100      |        | 105      |         | 177              |         |

Life-history traits include diameter growth rates (DGR), biomass growth rates (BGR) and mortality rates (M) of trees  $\geq 100$  mm diameter at breast height (DBH) and the maximum height of a species recorded in the 50-ha plot (H<sub>max</sub>). The key functional traits serve as independent variables and are wood density (mean of the species WD<sub>m</sub>), leaf nitrogen concentrations (N<sub>leaf</sub>), leaf mass per area (LMA) and calculated hydraulic conductivity (Kh), for which also the interaction term with the size of the sampled tree (DBH<sub>s</sub>) was tested. ns, not significant; -, not included in model (see the Materials and Methods section). For growth and mortality only species with > 49 observations were selected. All data except WD and H<sub>max</sub> were log-transformed.



**Fig. 4** Principal component analysis (PCA) of life-history traits, wood and leaf traits for 98 tree species from a Panamanian wet forest. Values in parentheses in the axis labels are percentages explained by the first two components.  $DBH_s$ , diameter at breast height of the sampled individual;  $Kh$ , calculated hydraulic conductivity;  $WD_m$ , mean wood density of the species;  $N_{leaf}$ , leaf nitrogen concentration;  $LMA$ , leaf mass per area;  $LA$ , leaf area;  $DGR$ , relative diameter growth rates;  $BGR$ , relative biomass growth rates;  $M$ , mortality rates. All demographic rates are for trees  $\geq 100$  mm  $DBH$ . See Supporting Information Table S1 for species scores.

and to water transport capacity ( $F$ ) may trade-off wood cross-sectional area in the chaparral plants with greater fractions of wood dedicated to both functions.

Why are  $WD$  and  $F$  unrelated in humid tropical forest trees? Cell walls contribute to wood biomass and thus  $WD$ , whereas cell lumina do not.  $WD$  must therefore be positively related to the fraction of cell walls and negatively to lumina. If vessel lumen fraction is not a driver of  $WD$ ,  $WD$  must be driven by the lumen or wall fraction of other cell types. The main driver of  $WD$  appears to be fibre wall thickness (Jacobsen *et al.*, 2007; Martínez-Cabrera *et al.*, 2011) and a recent study found that the proportion of the cross-section occupied by all cell lumina or by fibre walls were the best predictors of  $WD$  (Fortunel *et al.*, 2014). It appears that most trees can regulate  $WD$  and thus mechanical support without compromising vessel lumen fraction and hydraulic conductivity. Therefore,  $WD$  or lumen fraction are unlikely to constrain  $Kh$ . The correlation between  $WD$  and  $Kh$  is unlikely to reflect a direct trade-off but instead might be an indirect consequence of correlations of both with growth rates, where low  $WD$  enables fast growth and high water transport capacity supplies productive leaves.

Do species with large vessels dedicate a lower fraction of wood area to water transport?

We found a strong negative correlation between  $VA$  and  $VD$  similar to previous results from a large global dataset (Zanne *et al.*,

2010); however, the slope and intercept of those relationships were significantly different (Fig. 1). At low  $VD$ ,  $VA$  is almost 50% lower in our dataset than in the global dataset. We asked if this might be because our data from Panama represent exclusively tropical trees. For 409 tropical species in the global database (identified by selecting species classified as tropical in a global wood density dataset; Zanne *et al.*, 2009), the slope of the  $VA$ – $VD$  regression was marginally different from the slope from our dataset ( $P = 0.053$ ), but regression intercepts differed significantly ( $P < 0.001$ ) and  $VA$  at a given  $VD$  was still almost 50% lower in our dataset than in the global dataset.

It is difficult to assess the cause of this difference between datasets. We measured vessel lumen area and use mean diameter of individual vessels, whereas some studies in the global dataset report a range or the average of larger or smaller vessels. Moreover, the global dataset contains an unknown number of climbers, which often have large vessels (Carlquist, 1988) and a higher vessel density at a given vessel size (Jiménez-Castillo & Lusk, 2013). Including lianas in a dataset would thus result in disproportionately large vessels at the lower end of vessel densities, which is where our data differ most from the global dataset (Fig. 1). Datasets potentially obtained with different methods or from different growth forms should be compared with caution.

The implications for the vessel fraction ( $F$ ) might be more interesting than possible differences in the absolute size of the vessels. In the data compiled by Zanne *et al.* (2010) with a slope of  $-1$  for the regression between  $\log VD$  and  $\log VA$ ,  $F$  does not change along the  $VA : VD$  axis. By contrast, we found an increase in  $F$  in Panamanian trees with smaller and more numerous vessels (Table 2), and a slope of the regression between  $\log VA$  and  $\log VD$  of  $-0.85$ , which is similar to that obtained from 42 species from a tropical rainforest in Bolivia ( $-0.87$ ; data provided by L. Poorter). Because doubling vessel lumen area has a greater effect on  $Kh$  than doubling vessel density, species with few large vessels have higher  $Kh$  than species with many small vessels even though the total area dedicated to vessels is lower.  $Kh$  would be even larger in species with large vessels if  $F$  were constant over the range of vessel sizes and densities (Fig. 1). Apparently, species with larger vessels can reduce total lumen area.

Does phylogeny constrain relationships between wood traits and growth strategies?

Wood structure changes through evolution (Carlquist, 1975) and wood traits carry a strong phylogenetic signal. Based on a study of the California woody flora but not on statistical tests, it was suggested that vessel density evolves more rapidly than vessel area (Carlquist & Hoekman, 1985). We could not confirm this, as  $VD$  and  $VA$  both had similar phylogenetic signals. Interestingly, whereas phylogenetic signal was particularly high for structural traits ( $WD$ ,  $VA$  and  $VD$ ), it was substantially lower for  $Kh$ , which thus appears to be less constrained by evolution than vessel size and numbers. Hydraulic conductivity can be modulated by a combination of vessel size and area, and a small change in vessel area has a large effect on  $Kh$ . For this reason,  $Kh$  appears to be relatively unconstrained phylogenetically.

The relationship between wood traits and growth rates is also largely independent of phylogeny because the PIC regressions were mostly similar to species-wise regressions (Table 2). Likewise, whereas families differed strongly in individual traits such as VA, VD, F and Kh, the tight correlation between VA and VD also did not differ between families. Thus, whereas the variation in wood structure among species is large and constrained by phylogeny, the strategies of adjusting wood to enable fast growth are similar for unrelated species. Consequently, wood traits appear to be good predictors of growth strategies.

### Does the relationship between tree size and wood structure invalidate correlations with life-history traits?

The relationship between wood structure and life-history traits might be affected by differences between the mature forest population on Barros Cerrado Island (BCI), where we obtained demographic traits from, and the late secondary forests off BCI, where wood samples were collected from. Many wood traits change with tree size and/or age (Lachenbruch *et al.*, 2011), but whereas the wood samples were obtained from a younger forest than the one on BCI, the sample trees were mature trees and well within the size range of trees on BCI. In trees of a given size, wood traits can also differ if trees are growing under different conditions (Zobel & van Buijtenen, 1989), for instance growing isolated rather than in a closed forest. Because the late secondary forest was closed and of similar stature to the primary forest on BCI, and we used the outer wood – that is, the youngest part produced when the forest was already closed – we think this is unlikely to affect the relationship between the wood and life-history traits observed. Also, within-species variation was much lower than among-species variation and there was no or only a very small spatial effect on wood traits (see Notes S1), thus the sampling location appears unlikely to have affected the outcome of our study.

Correlations between Kh, F or VD with tree size were about twice as strong when using diameter at breast height for the sample rather than maximum for the species ( $DBH_s$  rather than  $DBH_{max}$ ) (Fig. 4). Although the effect of tree size on wood structure is well known and can be studied readily via radial changes from the pith towards the cambium, tree size has often been ignored in interspecific comparisons of wood structure and relationships with other traits. Size-related changes occur because trees adjust wood structure according to the changing requirements imposed by the environment and ontogenetic stage (Lachenbruch *et al.*, 2011). For instance, conduit lumen diameter tends to increase from juvenile wood to mature wood (Leal *et al.*, 2007; Christensen-Dalsgaard *et al.*, 2008; Lachenbruch *et al.*, 2011). This ontogenetic increase compensates for the higher resistance imposed by a longer pathway in tall trees (Tyree & Zimmermann, 2002). This is often presented as a difference between juvenile and mature wood, but the change can be gradual and can take place over several decades (Tsuchiya & Furukawa, 2010; Schuldt *et al.*, 2013).

If individual tree size is ignored, we may lose half the predictive power of functional traits (Fig. 4) or find and interpret

differences among species that are in fact differences among trees of different sizes that disappear when tree size is included. Based on our finding that correlations between wood anatomical traits and tree size were much stronger for the size of the sample tree than for the maximum size achieved by the species, one may question previous interpretations of similar correlations (Poorter *et al.*, 2010; Russo *et al.*, 2010; Fan *et al.*, 2012). Vessels and Kh reported from tree species that can attain a large size might be large because individuals sampled from these species tend to be large, and vessel size and Kh increase with tree size. Likewise, the widely held assumption that dryland plants have smaller vessels than plants from humid regions (Carlquist & Hoekman, 1985) might be the indirect result of associations between tree size and moisture availability, with smaller trees from drier regions, and between tree size and vessel diameters, with smaller plants having narrower vessels (Olson & Rosell, 2013). This calls for a re-thinking of the supposed benefits of small vessels.

Could the significant correlation between hydraulic conductivity and life-history traits also disappear when including tree size as a controlling variable? Although  $DBH_s$  is strongly correlated with Kh, the interaction between Kh and  $DBH_s$  did not significantly influence the relationship between Kh and growth rates (Table 3). The relationship between Kh and mortality was insignificant whether or not tree size was included. Only for maximum height of a species recorded in the 50-ha plot ( $H_{max}$ ) did we find a significant  $DBH_s \times Kh$  interaction, but  $H_{max}$  and Kh were still significantly correlated. The correlation between maximum tree size and Kh reported (Poorter *et al.*, 2010) might result from sampling larger individuals in species that reach greater maximum size and the scaling of vessel size with tree size (Olson & Rosell, 2013). Still, efficient water transport is important for trees that grow tall as well as for species with high growth rates.

Trees also show strong ontogenetic changes in demographic traits, and functional traits predict differences in growth trajectories among species (Héroult *et al.*, 2011; Rüger *et al.*, 2012). It would be interesting to compare such ontogenetic changes in demographic traits with possible ontogenetic changes in functional traits. For instance, species with low WD had the greatest potential to modulate their growth (Héroult *et al.*, 2011; Rüger *et al.*, 2012), and these species also tend to show the strongest radial variation in WD (Hietz *et al.*, 2013). Although the size of individual trees explained a large portion of the variation in wood traits (Fig. 3), information on ontogenetic changes in wood structure within a species is scarce. As with WD, species are likely to differ in their radial adjustments of Kh and other wood traits. An analysis of ontogenetic changes of wood traits for a wide range of species would help to better understand the functional significance of the traits as well as the life histories of the trees. Because wood structure is conserved (unless a tree rots), analysing radial changes in vessels or other components from the pith to the bark provides an easy pathway to study such ontogenetic adjustments.

### Which traits best explain life histories?

We found that mortality rate (M), diameter growth rate (DGR) and maximum tree size all scaled negatively with WD



(Table 2; Fig. 3), which agrees with previous studies (Wright *et al.*, 2010; Martínez-Cabrera *et al.*, 2011; but see Fan *et al.*, 2012). Low WD enables rapid DGR because less biomass is required per volume grown. Surprisingly, for the question which trees efficiently produce biomass, we found that wood density was positively correlated with biomass growth rate (BGR), although the explanatory power of the multiple regression model for BGR was low (Table 3). This is unexpected because species with lower WD are often light-demanding with higher rates of photosynthesis (Santiago *et al.*, 2004; Meinzer *et al.*, 2008a). A positive relationship between WD and biomass growth was also found on relatively fertile soils in the Peruvian Amazon (Keeling *et al.*, 2008). Keeling *et al.* offer two possible explanations for this: either species with high WD have deeper crowns and longer leaf lifespan, so that the overall carbon gain of their leaves may exceed that of lower WD species; or species with lower WD have higher rates of carbon loss through greater turnover of leaves or roots or through higher respiration rates. We also note that the relationship between WD and photosynthesis may be weaker than previously believed. This possibility is supported by the relative independence of wood and leaf traits including no significant relationship between WD and leaf nitrogen (N) (Baraloto *et al.*, 2010). Unfortunately, many studies on tree growth evaluate only DGR. Calculating BGR would provide additional insight into the functional significance of traits.

WD was the best predictor of M. This may have multiple functional explanations, which are hard to tease apart in ecological studies because WD is related to mechanical strength, fungal resistance and cavitation resistance. At the study site in Panama, trees with low WD more commonly snapped whereas trees with high WD were uprooted (Putz *et al.*, 1983), and in Amazonia species with lower wood density had higher drought-related mortality (Phillips *et al.*, 2010). Several mechanisms are likely to be responsible for the relatively strong relationship between WD and M.

Kh is known to be related to diameter growth, but also varies with tree size, which may have confounded previous analyses (Poorter *et al.*, 2010; Fan *et al.*, 2012). Both studies used pairwise correlations including only wood traits to predict growth. Because Kh is affected by the size of the individual tree, our multiple regression models initially included a  $\text{Kh} \times \text{DBH}_s$  interaction term but this was significant only for  $H_{\text{max}}$ . Apart from WD, the only leaf or wood traits with a significant effect on diameter as well as biomass growth in multiple models were leaf N concentration and Kh. Leaf N is strongly related to photosynthesis (Wright *et al.*, 2004) and high water transport rates are necessary to supply productive leaves. Of all variables tested, Kh had the strongest relationship with growth rates, possibly because hydraulic conductance integrates transpiration per leaf area and total leaf area. For instance, Kh per sapwood as well as per leaf area is correlated with maximum photosynthesis, stomatal conductance, photosynthetic nutrient-use efficiencies as well as growth rates in 17 dipterocarp trees (Zhang & Cao, 2009). Plants generally show a high coordination between hydraulic and photosynthetic capacities (Brodribb, 2009).

We note, however, that Kh per sapwood area is not the same as water consumption per tree. The capacity of a stem to

transport water equals the Kh per sapwood area times the total sapwood area. Interestingly, individual tree absolute biomass growth was best explained by sapwood area, which is interpreted as a positive effect of stem water storage (van der Sande *et al.*, 2015), but could also result from a correlation between hydraulic conductance and sapwood area. Comparisons with tree water use would help to elucidate the causal relationship between Kh and growth.

## Conclusions

Wood structure carries a strong phylogenetic signal, which means that the capacity for adaptations in the evolutionary short term is limited. However, wood traits evolve in a coordinated way and the fact that small changes in vessel size result in large changes in Kh means that trees are rather flexible in adjusting their hydraulic capacity. This is important during ontogeny, because tall trees can transport water more efficiently, and during evolution, because the water supply can be adjusted to the requirements of different growth rates. Of all wood and leaf traits, Kh was the best predictor of growth rates. However, because Kh also scales with tree size, the size of the sampled tree should be included in analyses of wood functional traits.

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## Author contributions

P.H. designed the study, analysed the data and wrote the first draft of the manuscript; S.R. and U.H-S. prepared and analysed wood sections; S.J.W. provided wood samples, data on leaf functional traits and life-history traits and contributed to data analysis, writing and interpretation.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Phylogenetic relationship of the tree species analysed from Panama.

**Table S1** Species scores of the principal component analysis in Fig. 4.

**Notes S1** Evaluation of the potential effect of within-species and spatial variations.

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