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Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density

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Summary

1. Stem xylem characteristics have a great impact on growth and adult stature of trees because of their role in mechanical support, long-distance water transport and whole-plant carbon allocation. Yet, despite the potential causal link between xylem traits and plant growth/adult stature, most studies have tried to link wood density, an indirect but easy to measure proxy for wood properties, to tree growth and size.

2. To determine whether xylem traits outperform wood density as predictors of tree growth and stature, we evaluated the covariation among wood density, xylem anatomical traits, tree diameter growth rate and adult stature in 40 Asian tropical tree species through principal component analyses and through bivariate correlation, both across species and across phylogenetically independent contrasts.

3. Vessel diameter exhibited a tight negative relationship with vessel frequency. Wood density showed a significant correlation with vessel diameter and density, but not with vessel fraction. Most correlations between functional traits indicate adaptive coordination, demonstrated by significant correlations between phylogenetically independent contrasts.

4. Across species, diameter growth rate and adult stature were positively correlated with vessel lumen diameter and potential hydraulic conductivity, but not with wood density. Thus, our results suggest that xylem anatomical traits that are linked to hydraulic conductivity are better predictors of tree growth rate and adult stature than wood density.

5. *Synthesis*. We found that xylem anatomical traits have a more significant influence on whole-plant performance due to their direct association with stem hydraulic conductivity, whereas wood density is decoupled from hydraulic function due to complex variations in xylem components.

Key-words: long-term tree growth, phylogenetically independent contrasts, plant development and life-history traits, tropical rain forest, vessel diameter, whole-plant performance, xylem anatomy

Introduction

Wood characteristics, especially wood density, have been traditionally regarded as core plant functional traits because of their importance for mechanical support, defence, architecture, hydraulics, carbon gain and growth potential of plants (Castro-Díez *et al.* 1998; King *et al.* 2006; Chave *et al.* 2009; Onoda, Richard & Westoby 2010; Zanne & Falster 2010). Low wood density is often associated with fast growth (Enquist *et al.* 1999; Muller-Landau 2004; Osunkoya *et al.* 2007), whereas high wood density is associated with greater stress tolerance and survival because of its association with higher hydraulic safety (Hacke *et al.* 2001; Sperry, Meinzer & McCulloh 2008) and stronger biomechanical strength (van Gelder, Poorter & Sterck 2006; Jacobsen *et al.* 2007). Thus, several lines of evidence suggest that wood density is related to a fast-to-slow growth-rate continuum, whereby species with denser wood tend to have slower growth, higher survival and greater shade tolerance than species with softer wood (King *et al.* 2005, 2006; Chave *et al.* 2006).

However, across a wide range of species, wood density is usually weakly correlated with growth rate (Chave *et al.* 2009;

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Poorter *et al.* 2010). For example, Nascimento *et al.* (2005) found that the association between wood density and growth rate disappeared altogether when a few gap-demanding species were removed from the analysis. These mixed results may arise because wood density is a complex trait and the same wood density can be achieved by various combinations of vessel diameter, vessel frequency and wood fibre traits (Zanne *et al.* 2010), each of these traits has different functional consequences for growth (Preston, Cornwell & DeNoyer 2006; Russo *et al.* 2010).

Wood density in vessel-bearing angiosperms is determined by properties of the vessels, the matrix of fibres and the parenchyma cells surrounding them (Baas *et al.* 2004). Wood composed of closely spaced large vessels will have low density with high hydraulic conductivity, whereas wood composed of small vessels spaced widely within a fibre matrix will be dense with low hydraulic conductivity (Preston, Cornwell & DeNoyer 2006). Wood density is expected to be inversely related to total fibre area (Preston, Cornwell & DeNoyer 2006; Jacobsen *et al.* 2007), but this relationship has not been found by other studies (Martínez-Cabrera *et al.* 2009; Poorter *et al.* 2010). Therefore, it is especially instructive to divide variation in wood density into its component parts and examine their ecophysiological consequences for whole-plant performance. However, few studies have investigated more detailed xylem anatomical traits to link wood properties with whole-plant performance (Castro-Díez *et al.* 1998; Preston, Cornwell & DeNoyer 2006; Poorter *et al.* 2010; Martínez-Cabrera *et al.* 2011).

It is well known that canopy photosynthesis is largely under the control of hydraulic architecture (Hubbard *et al.* 2001; Meinzer 2003; Santiago *et al.* 2004; Ishida *et al.* 2008). Vessel lumen area strongly affects sapwood-specific conductivity because conductive capacity scales with vessel diameter to the fourth power (Tyree & Ewers 1991). Thus, a positive correlation between vessel size and growth rate is expected, because wider vessels allow greater rates of transpiration and photosynthesis (Brodribb, Holbrook & Gutierrez 2002; Zhang & Cao 2009; Meinzer *et al.* 2010). Meanwhile, wider vessels, which are associated with lighter wood, are more vulnerable to cavitation (Davis, Sperry & Hacke 1999). An important mechanism facilitating drought tolerance is a 'safe' hydraulic system consisting of smaller and denser vessels (Baas *et al.* 2004). However, these traits compromise the hydraulic efficiency via increased resistance to water transport (Hacke *et al.* 2006; Pratt *et al.* 2007). In this way, safety from embolism limits canopy productivity and should result in lower growth rates. However, comparative studies combining growth data from long-term plots with xylem traits are rare.

Adult stature, or maximum plant height, is another complex trait that is associated with plant light interception (King *et al.* 2005, 2006). It is often hypothesized that there should be a systematic relationship between adult stature and ecophysiological traits (e.g. wood properties and hydraulic xylem network), particularly in a closed canopy system like tropical rain forest where competition for light is severe (Thomas 1996; King *et al.* 2006). However, reported relationships between adult stature and wood density are mixed. For example, negative correlations between wood density and adult stature were found within shade-tolerant species (Falster & Westoby 2005; Poorter, Bongers & Bongers 2006), but this relationship vanished when pioneer and shade-tolerant species were pooled (van Gelder, Poorter & Sterck 2006; Aiba & Nakashizuka 2009). On the other hand, maximum height has been found to be associated with vessel size and frequency across a wide range of woody plants (Preston, Cornwell & DeNoyer 2006; Martínez-Cabrera *et al.* 2011). Chave *et al.* (2009) also suggested that taller angiosperms have wider vessels because they are more efficient for water transport per unit area, leaving more space for fibres for mechanical support.

Trait correlations observed across taxonomically diverse species do not necessarily reflect coordinated evolutionary changes or adaptive functional trade-offs (Felsenstein 1985; Ackerly & Reich 1999). Some observed cross-species correlations between traits may simply be due to a common ancestry (non-independence of species) (Garland, Harvey & Ives 1992). Thus, the inclusion of phylogenetically independent contrasts provides a more powerful quantitative test for correlated evolutionary change underlying contemporary trait variation and covariation (Ackerly & Donoghue 1998; Maherali, Pockman & Jackson 2004).

In the present study, we examined the covariation in wood density and xylem anatomical traits, together with tree growth rate and adult stature among 40 coexisting tree species in an Asian tropical forest, southwestern China. By using phylogenetically independent contrasts, we examined whether these traits show coordinated variation at multiple divergences across the phylogenetic tree. We aim to (i) evaluate the covariation of xylem anatomical traits among co-occurring tree species, and its potential in constraining variation in high-order traits, such as tree growth rate and adult stature, and (ii) test the hypothesis that xylem anatomical traits are better predictors of tree growth rate and adult stature than wood density.

Material and methods

STUDY SITE AND SPECIES

This study was conducted at Xishuangbanna Tropical Botanical Garden (XTBG, 21°41′ N, 101°25′ E, altitude 570 m) in the southern Yunnan Province, Southwestern China. The region has a typical tropical monsoon climate and thus has a distinct dry season from November to April. Mean annual precipitation is about 1560 mm, of which about 80% falls during the rainy season from May to October. Mean annual temperature is 21.7 °C with a monthly mean temperature being 15.9 °C during the coldest month (December) and 25.7 °C during the warmest month (June).

In this study, we selected 40 co-occurring tree species belonging to 39 genera, 24 families and 11 orders (Fig. 1). This set of species was well distributed over the phylogeny and covered different leaf habits (30 evergreen and 10 deciduous species) and successional stages (nine early-successional and 31 late-successional species). Most (38) of the species had diffuse-porous woods (Table S1 in Supporting Information). All these species are common in the natural forests around XTBG. During the 1990s, XTBG conducted a comprehensive investigation of wood properties for over a hundred broadleaf tree species growing in the Xishuangbanna region. The investigated properties include species distribution and habitats, macroscopic and micro-

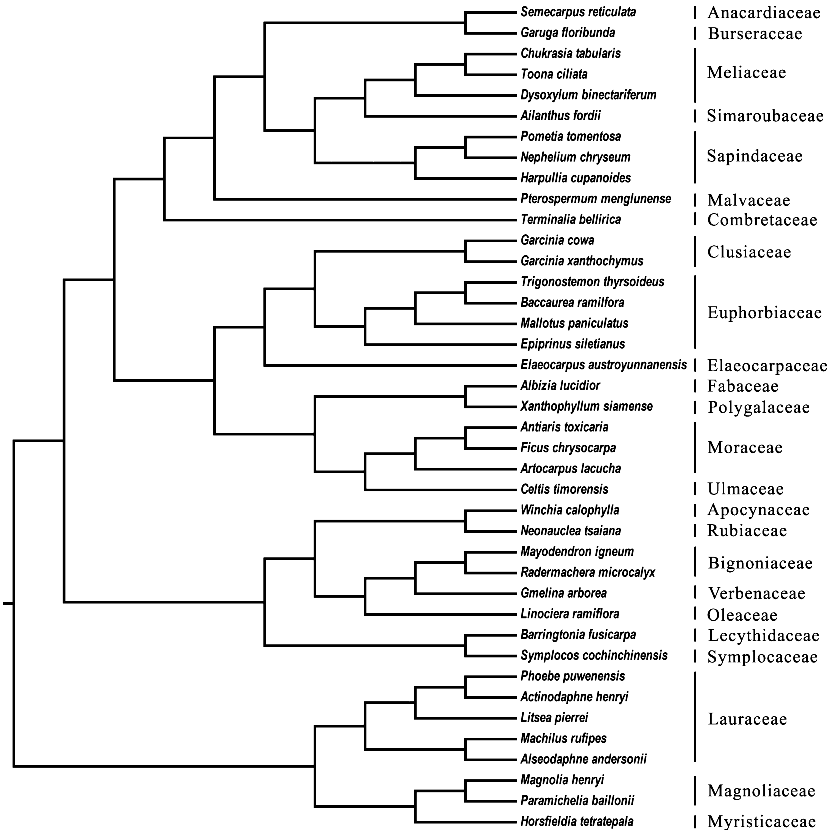

Fig. 1. Phylogenetic relationship of the 40 tropical tree species. The backbone is based on the Angiosperm Phylogenetic Group III classification (APG III; Webb, Ackerly & Kembel 2008). Family divisions are indicated by the broken line on the right side of the figure.

scopic structures, and wood density and mechanical properties (Zhang *et al.* 1989; Ye, Mo & Zou 1999).

WOOD DENSITY AND ANATOMICAL TRAITS

Wood material of the 40 studied species was collected from XTBG or nearby natural forests for three individuals per species. One sample per tree was taken from the main trunk at breast height (1.3 m) with a chisel. Wood fresh volume was measured using the water displacement method, after which the samples were oven-dried for at least 48 h at 70 °C. Wood density (WD, g cm^{-3}) was determined as wood dry mass per unit of fresh volume. Wood samples were then softened by soaking in a solution of glycerine and ethanol (1 : 1 by volume) for three to four months. One transverse section (15–50 μm thick) per wood sample was made with a sliding microtome and then stained with safranin and embedded in neutral balsam. Cross-sections were made and dry-preserved by XTBG staff (Zou SQ, pers. comm.).

Cross-sections of the 40 tree species were retrieved from XTBG and then imaged using a digital camera (DFC 295, Leica, Germany) mounted on a microscope (DM 2500, Leica, Germany). Two to three slides per species were taken at 50× magnification and three to five images were taken per slide. Images were analysed using the IMAGEJ program (http://rsb.info.nih.gov/ij/index.html). The lumen diameter (major and minor axis) and total lumen area of all individual vessels in each cross-sectional image were measured. For each species, at least 50 vessels (> 550 for small vessels) were analysed. Since vessels are not exactly circular but mostly elliptical, the diameter of each vessel was calculated as $D = [32(ab)^3/(a^2 + b^2)]^{1/4}$, where a and b are the major and minor axis dimensions, respectively (Lewis 1992). Vessel diameters were averaged for each image field. Vessel density (VD) was calculated as number of vessels per unit wood area (mm^{-2}). Vessel fraction (VF, %) was determined as the ratio of total vessel lumen area to xylem area. According to the Hagen–Poiseuille law (Tyree & Ewers 1991), the potential hydraulic conductivity (K_p, kg m^{-1} MPa^{-1} s^{-1}) was calculated as $K_p = (\pi\rho/128\eta A)[\Sigma D_i^4]$ for $i = 1$ to n vessels in each field, where A is field area, ρ is the density of water (998.2 kg m^{-3} at 20 °C) and η is the viscosity of water (1.002×10^{-9} MPa s^{-1} at 20 °C).

DIAMETER GROWTH RATE AND ADULT STATURE

We selected forestry census data of the 40 tree species from the two permanent plots dedicated to long-term ecological research managed by XTBG since the mid-1990s (Table S2 in Supporting Information). Plot I (1 ha) was established in 1994, while plot II (0.5 ha) was established in 2002. The two plots are adjacent to each other (< 10 km) and have similar climate and soil conditions, as well as tree species diversity. At each plot, trees of diameter at breast height (DBH) ≥ 5 cm were mapped, tagged, identified and measured yearly for their DBH (mm) and height (m).

For each tree, the DBH at consecutive censuses was regressed against the corresponding measurement date. The corresponding slope was used to obtain an annual diameter growth rate (GR, mm yr^{-1}). Trees included in this analysis had at least six DBH measurements. Trees with negative or anomalous growth, assuming here to be caused by measurement error, were excluded from the analyses. Species-specific growth rate means were obtained for all 40 species from a total of 795 individuals (Table S3 in Supporting Information).

For the selected species, maximum (potential) plant height (H_{max}) was estimated from $H = H_{max}[(1-\exp(-aDBH^b)]$, where H is tree height in metres, DBH is diameter at breast height in centimetres and a and b are allometric coefficients that approach values of standard allometric constants for small values of H (Thomas 1996). For tree species that did not show a clear asymptote, we used height at the maximum observed DBH as predicted by species-specific regression equations, rather than the estimated asymptote, as the maximum height (Poorter, Bongers & Bongers 2006; Aiba & Nakashizuka 2009).

CONSTRUCTION OF THE PHYLOGENETIC TREE

A phylogenetic tree at family level was first constructed using PHYLOMATIC, which is based on the Angiosperm Phylogeny Group III classification of angiosperms (APG III; http://www.phylodiversity.net/phylomatic/). To resolve the phylogenetic relations of species belonging to the same families, nuclear ITS sequences were retrieved for 12 tree species belonging to three families (5.8s ribosomal RNA for Lauraceae and Sapindaceae, 18s ribosomal RNA for Euphorbiaceae) from the GenBank (http://www.ncbi.nlm.nih.gov/genbank/). The ITS sequences were aligned, and the phylogenetic relationships were built by neighbour-joining (NJ) method using the MEGA program (version 4.0; Tamura *et al.* 2007). The final phylogenetic tree included all the 40 tree species (Fig. 1). Conservative branch lengths of the phylogenic tree were assigned using the BLADJ function of PHYLOCOM (Webb, Ackerly & Kembel 2008).

STATISTICS AND PHYLOGENETIC COMPARATIVE METHODS

To increase the normality of distributions, the original data were $\log_{10}$-transformed (Kerkhoff & Enquist 2009). Pearson's correlations were calculated for all pairwise combinations of traits. Bivariate relationships were analysed using standardized major axis (SMA) regression, or model II regression, using the SMATR software (http://www.bio.mq.edu.au/ecology/SMATR/). The SMA is more suitable than regression model I for examining the scaling relationship between two variables that are both measured with error (Warton *et al.* 2006). To describe correlation patterns among multiple traits, principal components analyses (PCA) were performed for seven traits of all the 40 tree species, using both original trait data and phylogenetically independent contrasts (PICs).

We tested the phylogenetic signal using the *K*-statistic and a randomization test implemented via phylogenetically independent contrasts (Blomberg, Garland & Ives 2003) using R v2.12.0 (R Development Core Term 2008, package 'picante'). Phylogenetically independent contrasts (PICs) for all the functional traits were calculated using the developed reference phylogeny of the 40 species (Felsenstein 1985; Garland, Harvey & Ives 1992). Independent contrasts were calculated as the difference in trait means of two daughter nodes or tips divided by the expected amount of change, which is the square root of the branch length separating the two taxa. This provides $N-1$ contrasts, where N is the number of tips in the phylogeny ($N = 40$). All trait data were $\log_{10}$-transformed prior to contrast calculation. To examine the coordination among functional traits throughout their phylogeny, we performed a correlation analysis on calculated PICs by forcing lines through the origin (Garland, Harvey & Ives 1992), using CACTUS 1.13 (comparative analysis of continuous traits using statistics, Schwilk & Ackerly 2001). A significant correlation between PICs for two traits indicates that these traits have undergone changes in similar direction and magnitude across the phylogeny and supports a possible functional link between these traits (Jacobsen *et al.* 2007).

Results

ASSOCIATIONS AMONG WOOD TRAITS

Xylem traits varied substantially across the 40 tree species (Tables S1 and S4 in Supporting Information): wood density (WD) varied 2.5-fold (0.34–0.86 g cm^{-3}), vessel diameter (D) varied 3.7-fold (61.8–226.2 μm), vessel density (VD) varied 12-fold (2.2–24.2 vessels per cm^{-2}) and potential hydraulic conductivity (K_p) varied 35-fold (9.5–332.5 kg m^{-1} s^{-1} MPa^{-1}). Vessel fraction (vessel/xylem ratio, VF) only showed a moderate variation (4–20%) despite a wide range of vessel densities. Early-successional species had, on average, wider vessels, lighter wood, higher K_p and growth rates compared with late-successional species. However, only the differences in K_p and WD were statistically different between these two successional stage categories ($P < 0.05$).

Results of the principal component analysis showed that the first axis explained 45.4% of the variation among the seven traits and was mostly associated with wood density (WD), vessel density (VD) and vessel lumen diameter (D) (Fig. 2a). The second axis explained 22.8% of the variation and was associated with water transport capacity (D, K_p), growth rate (GR) and adult stature (H_{max}) (Table S5 in Supporting Information). The results of the PCA based on phylogenetically independent contrasts (PICs) were generally consistent with the results of the conventional PCA (Fig. 2b).

Species with higher vessel density (frequency) had significantly narrower vessel lumens and greater vessel fractions (vessel area per unit xylem area), whereas vessel diameter and vessel fraction were unrelated (Table 1, Fig. S1 in Supporting Information). Potential hydraulic conductivity (K_p) was positively related to vessel lumen diameter and vessel fraction, but negatively related to vessel density (Fig. S2 in Supporting Information). Wood density was correlated negatively with vessel lumen diameter and positively with vessel density, but not with vessel fraction (Fig. S3 in Spporting Information). Most of the correlations based on PICs were consistent with the cross-species correlations, except that the negative correlation between WD and K_p only became significant when phylogeny was incorporated into the analysis (Table 1, Figs S1–S3 in Supporting Information).

CORRELATIONS BETWEEN XYLEM TRAITS AND WHOLE-PLANT PERFORMANCE

Stem diameter growth rate was positively correlated with vessel diameter and potential hydraulic conductivity, both for cross-species means and PICs (Table 1, Fig. 3). Growth rate was inversely correlated with vessel density, but this correlation became non-significant when analysed using phylogenetically independent contrasts (Fig. 3b,f). Adult stature was positively related to vessel diameter and potential hydraulic conductivity,

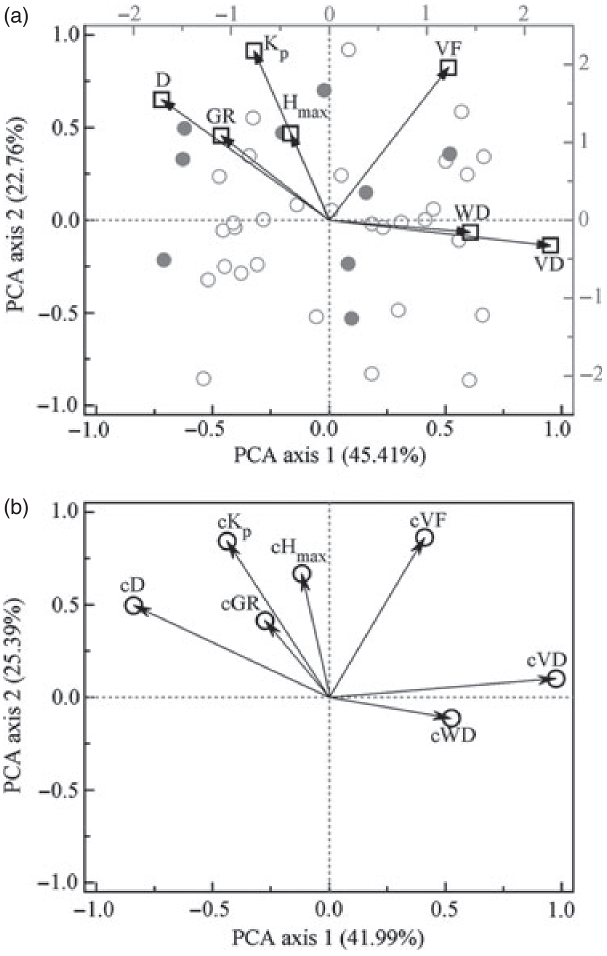

Fig. 2. Principal component analyses (PCA) on cross-species means (a) and phylogenetically independent contrasts (b) for seven traits among 40 tropical tree species. Grey (early-successional) and white (late-successional) circles indicate the loadings of individual species on these axes. *D*, vessel diameter; VD, vessel density; VF, vessel fraction; K_p, potential hydraulic conductivity; WD, wood density; GR, diameter growth rate; H_{max}, adult stature.

but not with vessel density or vessel fraction (Table 1, Fig. 4). On the other hand, neither growth rate nor adult stature was significantly correlated with wood density, both for cross-species and PICs comparisons (Figs 3 and 4). Growth rate showed a marginal positive correlation ($R = 0.26$, $P = 0.1$) with adult stature, and this relationship became more significant ($R = 0.28$, $P < 0.05$) when phylogenetically independent contrasts were used (Fig. S4 in Supporting Information).

Discussion

ASSOCIATIONS BETWEEN WOOD DENSITY AND VESSEL TRAITS

Wood density was expected to decrease with increasing vessel cross-sectional area (vessel fraction), as more open vessel lumen spaces should lead to less dense material (Preston, Cornwell & DeNoyer 2006). However, no significant correlation between wood density and vessel fraction was found across the 40 species in the present study (Fig. S3 in Spporting Information). Similarly, wood density of 42 Bolivian tree species was not correlated with either vessel fraction or fibre cross-sectional area (Poorter *et al.* 2010). Jacobsen *et al.* (2007) proposed that variation in wood density might be driven by fibre cell wall thickness, rather than by variations in fibre tissue area. Accordingly, Martínez-Cabrera *et al.* (2009) found that wood density of 61 shrub species was mainly driven by fibre characteristics, that is, denser woods were associated with smaller fibre lumens and higher fibre wall to lumen ratios. Wood density was negatively correlated with vessel diameter but positively correlated with vessel density (Fig. S3 in Supporting Information), which is consistent with a study based on 135 tree species in North America (Martínez-Cabrera *et al.* 2011).

CORRELATIONS BETWEEN XYLEM TRAITS AND GROWTH

Contrary to the hypothesis that wood density is a good proxy of tree species' position along a fast-to-slow growth continuum (Chave *et al.* 2006), we did not find significant correlation between wood density and diameter growth rate in the present study (Fig. 3). Although species with the lowest wood densities (early-successional) tend to grow faster, many species with

Table 1. Pearson's correlation coefficients and independent contrast correlation coefficients between xylem anatomical traits, wood density, growth rate and adult stature of 40 tropical tree species

	D	VD	VF	K_p	WD	GR	H_{max}
D		−0.831**	0.171	0.876**	−0.401**	0.515**	0.300*
VD	−0.785**		0.405**	−0.467**	0.428**	−0.435**	−0.190
VF	0.116	0.523**		0.617**	0.104	0.077	0.160
K_p	0.835**	−0.325*	0.633**		−0.261	0.440**	0.321*
WD	−0.402**	0.351*	0.016	−0.292*		−0.126	−0.104
GR	0.379**	−0.253	0.112	0.339*	0.169		0.260
H_{max}	0.321*	−0.060	0.345*	0.422**	−0.197	0.280*	

Data were log-transformed before analysis of Pearson's correlation and phylogenetically independent contrasts.
Correlations between species are given upper right of the diagonal, and correlations between phylogenetically independent contrasts (PICs) forcing lines through the origin are given lower left. *D*, vessel diameter (μm); VD, vessel density (mm^{-2}); VF, vessel fraction (%); K_p, potential hydraulic conductivity ($kg\ m^{-1}\ s^{-1}\ MPa^{-1}$); WD, wood density ($g\ cm^{-3}$); GR, diameter growth rate ($mm\ yr^{-1}$); H_{max}, adult stature (*m*). $N = 40$ for cross-species trait data and 39 for PICs. Traits that are significantly correlated are marked: $^{**}P < 0.01$; $^{*}P < 0.05$.

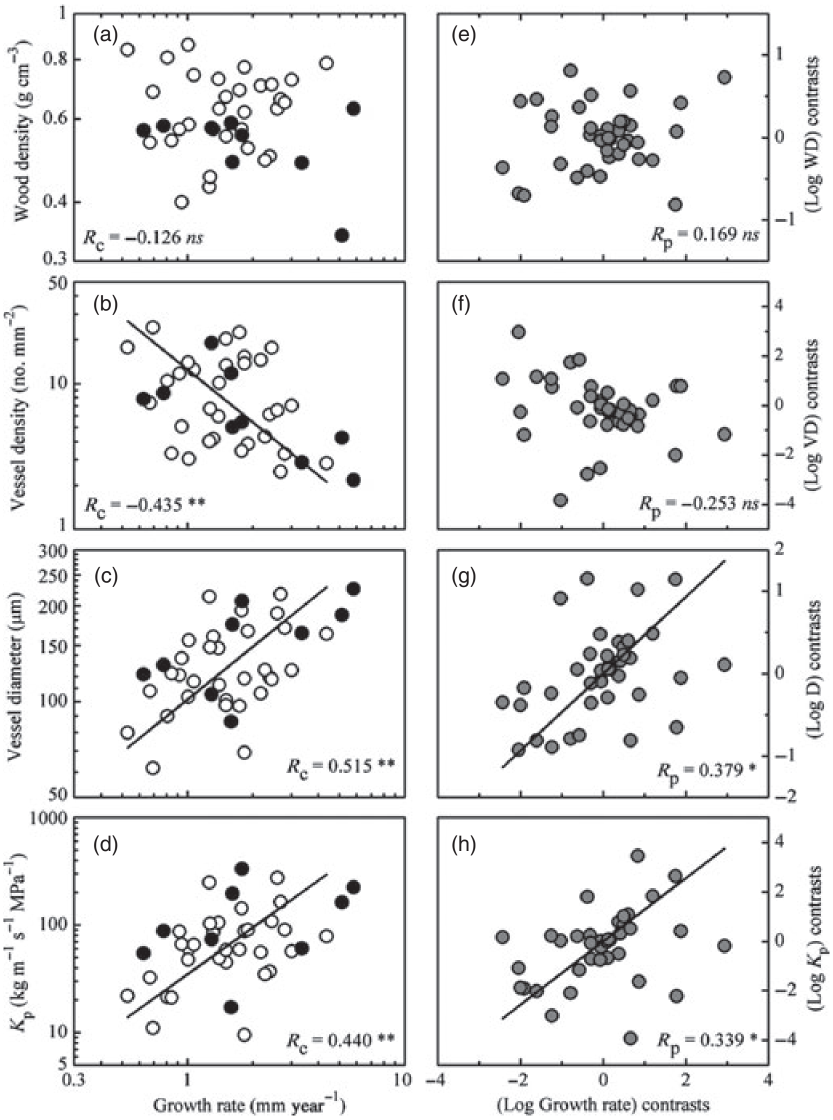

Fig. 3. Relationship between diameter growth rate (GR) and wood density (WD; a, e), vessel density (VD; b, f), vessel diameter (D; c, g) and potential hydraulic conductivity (K_p; d,h) for 40 tropical tree species. Black and white circles represent early-successional and late-successional species, respectively. Note the $\log_{10}$ scales in panels from (a) to (d). Standardized major axis (SMA) regression lines are shown for significant relationships only. Pearson's cross-species (R_c) and phylogenetically independent contrast (R_p) correlation coefficients are shown. *ns*, $P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$.

intermediate wood density had variable growth rates. Moreover, no significant relationships between wood density and growth rate were found within different groups of successional stages (earlier- or late-successional species) (Table S6 in Spporting Information). Similarly, wood density of terminal branches from 17 dipterocarp species was not correlated with either mean diameter or height growth rates (Zhang & Cao 2009). Even where a negative correlation between wood density and growth was found, it was often relatively weak (Nascimento *et al.* 2005; Osunkoya *et al.* 2007; Chave *et al.* 2009).

The lack of a strong correlation between wood density and growth rates is likely to have arisen from the fact that wood density is determined by both vessel and fibre properties (Martínez-Cabrera *et al.* 2009). The tight negative association between vessel size and vessel density (Fig. S2 in Supporting Information) constrains the variability of vessel fractions, and thus fibre cross-sectional area. Moreover, density of the matrix outside of the lumens may contribute considerably to variation in wood density, which allow our studied species to partially escape from the putative trade-offs involving wood density and conductivity (Hacke *et al.* 2006; Russo *et al.* 2010).

In this study, we found xylem anatomical traits were much better predictors of growth rate than wood density, which is consistent with their more direct and stronger correlation with hydraulic conductivity (Castro-Díez *et al.* 1998; Russo *et al.* 2010). The coordination of hydraulics and growth rate has been observed within dipterocarp species growing in a common garden (Zhang & Cao 2009) as well as species growing in native rain forest (Poorter *et al.* 2010), which is due to a strong hydraulic–photosynthetic coordination (Hubbard *et al.* 2001;

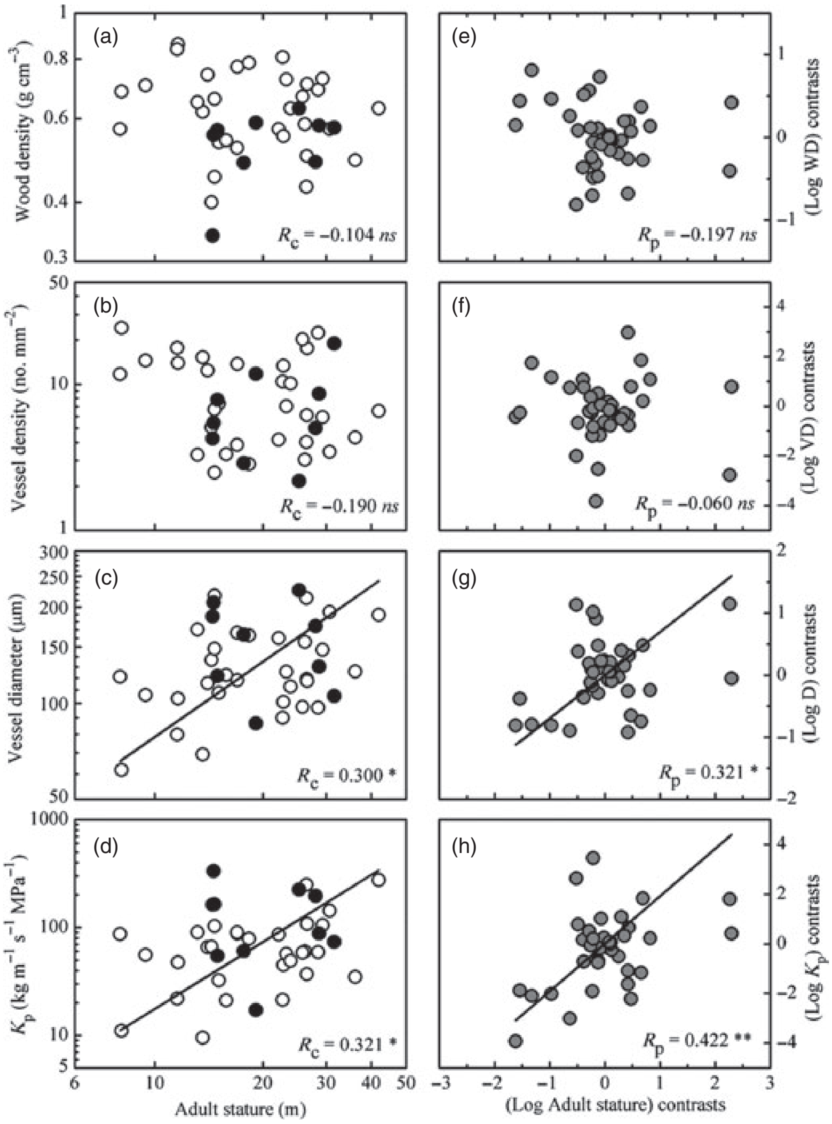

Fig. 4. Relationship between adult stature (H_{max}) and wood density (WD; a, e), vessel density (VD; b, f), vessel diameter (*D*; c, g) and potential hydraulic conductivity (K_p; d,h) for 40 tropical tree species. Black and white circles represent early-successional and late-successional species, respectively. Note the $\log_{10}$ scales in panels from (a) to (d). Standardized major axis (SMA) regression lines are shown for significant relationships only. Pearson's cross-species (R_c) and phylogenetically independent contrast (R_p) correlation coefficients are shown. *ns*, $P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$.

Santiago *et al.* 2004; Ishida *et al.* 2008). Tree species with larger but less dense vessels are generally associated with high potential hydraulic conductivity (Fig. S2 in Supporting Information). Higher water transport efficiency through the stem allows for higher stomatal conductance and crown photosynthetic rates, and hence higher potential growth rates (Brodribb, Holbrook & Gutierrez 2002; Meinzer *et al.* 2010).

CORRELATIONS BETWEEN XYLEM TRAITS AND ADULT STATURE

Both negative and positive interspecific relationships between wood density and stature have been reported. Negative correlations typically arise across light gradients within tropical forests (Thomas 1996), whereas positive correlations are associated with successional gradients (Falster & Westoby 2005). In each case, the relationship is mediated by a trade-off between wood density and growth rate. However, we found no significant correlation between wood density and adult stature, which is consistent with several other studies (Osunkoya *et al.* 2007; Russo *et al.* 2010; Martínez-Cabrera *et al.* 2011). We also found no evidence that the correlation between wood density and adult stature was mediated by a relationship between wood density and growth rate (Preston, Cornwell & DeNoyer 2006). Considering the large discrepancies among different studies, wood density may not necessarily have an intrinsic association with growth rate and adult stature. Instead, we found xylem anatomical traits directly associated with hydraulic conductivity are better predictors of growth rate and adult stature of tropical forest tree species.

Adult stature was positively correlated with vessel diameter and potential hydraulic conductivity (Fig. 4), which implies that tree species achieving greater heights require greater hydraulic capacity (Koch *et al.* 2004). Similarly, Zach *et al.* (2010) found that twig vessel diameter and sapwood-area-specific hydraulic conductivity significantly increased with tree height across eight common tropical rain forest tree species in Indonesia. A recent model has shown that optimal carbon allocation would produce stems that maximize conductivity (via large vessels) and minimize wood density while just maintaining adequate mechanical support (Taneda & Tateno 2004). Variation in vessel density may allow species to maintain sufficient wood density even while increasing lumen area (Preston, Cornwell & DeNoyer 2006).

PHYLOGENETIC SIGNAL AND CORRELATED EVOLUTION

Our analysis with and without the incorporation of evolutionary relationships was mostly consistent, indicating that the detected patterns reflect coordinated evolution. Moreover, the relatively low levels of phylogenetic signal of the seven studied traits (Blomberg's *K*-values < 1, Table S4 in Supporting Information) may result from the fact that the studied species are phylogenetically diverse (from many families), and thus common ancestral effect is minimal (Ackerly 1999). Vessel lumen diameter showed a strong negative contrast correlation with vessel frequency (Fig. 2), indicating that increases in vessel size during evolution have generally been accompanied by decreases in vessel density (Preston, Cornwell & DeNoyer 2006; Russo *et al.* 2010; Zanne *et al.* 2010). Recently developed metrics indicate that both vessel area and wood density show strong phylogenetic conservatism among 17 *Quercus* species in Florida (Cavender-Bares, Kitajima & Bazzaz 2004). Meanwhile, correlation between vessel density and growth rate became non-significant when PICs were used (Fig. 3b,f). These results are consistent with the findings of Carlquist & Hoekman (1985), who argued that vessel density changes more rapidly or is more evolutionarily labile, than vessel area.

Conclusion

Our analyses indicate that tree growth rate and adult stature are associated with xylem anatomical traits determining stem hydraulic capacity, but not with wood density. Our results also suggest that wood density is not a good proxy for tree species' position along a fast-to-slow growth continuum, which results from the fact that wood density is decoupled from hydraulic function due to complex variations of xylem components (vessel size, vessel density, fibre area and density). In contrast, xylem anatomical traits have a more significant influence on whole-plant performance due to their direct association with stem hydraulic conductivity and their important role in intermediating a suite of evolutionarily based functional trade-offs, which determine niche differentiation and functional diversity of tropical forest tree species.

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Supporting Information

The following Supporting Information is available for this article:

Figure S1. Cross-species (a) and phylogenetically independent contrast (b) correlations between vessel diameter and vessel density across 40 tropical tree species.

Figure S2. Relationships between potential hydraulic conductivity (K_{p}) versus vessel fraction (VF), vessel density (VD) and vessel diameter (D) for 40 tropical tree species.

Figure S3. Relationships between wood density and potential hydraulic conductivity (K_{p}), vessel fraction (VF), vessel density (VD) and vessel diameter (D) for 40 tropical tree species.

Figure S4. Cross-species and phylogenetically independent contrast correlations between growth rate and adult stature across 40 tropical tree species.

Table S1. List of wood density, wood anatomical and mechanical traits of 40 tropical tree species.

Table S2. Plots information for growth data.

Table S3. List of growth rate, adult stature and their calculation information for 40 tropical tree species.

Table S4. Statistics of the seven traits of 40 tropical tree species, as well as different successional stages (early- or late-successional).

Table S5. Eigenvalues and factor loadings of conventional and phylogenetic principal component analysis on seven traits of 40 tropical tree species.

Table S6. Pearson's correlation coefficients among xylem traits, growth rate and adult stature within different groups of successional stages.