The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species

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Summary

- In a comparative study of 42 rainforest tree species we examined relationships amongst wood traits, diameter growth and survival of large trees in the field, and shade tolerance and adult stature of the species.
- The species show two orthogonal axes of trait variation: a primary axis related to the vessel size–number trade-off (reflecting investment in hydraulic conductance vs hydraulic safety) and a secondary axis related to investment in parenchyma vs fibres (storage vs strength). Across species, growth rate was positively related to vessel diameter and potential specific hydraulic conductance (K_p), and negatively related to wood density. Survival rate was only positively related to wood density.
- Light-demanding species were characterized by low wood and vessel density and wide vessels. Tall species were characterized by wide vessels with low density and large K_p. Hydraulic traits were more closely associated with adult stature than with light demand, possibly because tall canopy species experience more drought stress and face a higher cavitation risk.
- Vessel traits affect growth and wood density affects growth and survival of large trees in the field. Vessel traits and wood density are therefore important components of the performance and life history strategies of tropical tree species.

Introduction

A perennial woody stem is the basic feature that sets woody plants aside from herbaceous plants. Recently, stem traits are emerging as core plant functional traits because of their importance for the stability, defence, architecture, hydraulics, carbon gain and growth potential of plants (Santiago *et al.*, 2004; Jacobsen *et al.*, 2008; Chave *et al.*, 2009). Wood density is often taken as a starting point to compare species, because it is easy to measure, readily available for a large number of species, and because it has strong ecological implications (Falster, 2006). Wood density partly underlies, for example, the growth–survival trade-off that is observed among woody plants (Kitajima, 1994; Kobe *et al.*, 1995;

Poorter & Bongers, 2006). Low wood density is associated with fast growth because of cheap volumetric construction costs of the wood, whereas high wood density is associated with high survival because of biomechanical and hydraulic safety (Putz *et al.*, 1983; Hacke *et al.*, 2001; Sterck *et al.*, 2006) and resistance against physical damage by herbivores, pathogens and falling woody debris (Augspurger & Kelly, 1984; Van Gelder *et al.*, 2006; McCarthy-Neumann & Kobe, 2008).

Analogously to specific leaf area for leaves, wood density is associated with a variety of morphological and physiological stem traits that are closely related to the functioning of trees. In angiosperm tree species, wood or xylem is built up of three different tissue types that fulfil different functions:

vessels provide longitudinal water transport; parenchyma as living, physiologically active cells provide carbohydrate storage and local radial transport; and fibres provide mainly strength. Investments in these different tissue types therefore imply trade-offs between the different functions they deliver. Such trade-offs, however, might be compensated by the size, number and structure of the elements that make up these tissue types. For example, hydraulic conductance depends not only on the stem cross-sectional area occupied by vessels but also on the size and number of these vessels. According to the Hagen–Poiseuille law, the hydraulic conductance scales with the fourth power of the vessel radius. Wider vessels therefore contribute to a larger hydraulic conductance (Sperry *et al.*, 2006) which, in turn, facilitates higher stomatal conductance and more photosynthetic carbon gain (Santiago *et al.*, 2004). By contrast, smaller vessels imbedded in a matrix of dense tissue lead to a higher hydraulic safety because of less risk of vessel implosion (Hacke *et al.*, 2001) and cavitation (as small vessels have lower risk of air-seeding because they have a smaller pit membrane area (Hacke *et al.*, 2006)).

The picture that emerges is that trees can solve strength and hydraulic limitations in several ways, but little is known how anatomical traits (co)vary across sympatrically occurring tree species. Some authors suggest that there is a spectrum in wood properties paralleling the economics spectrum found for leaves (Chave *et al.*, 2009), but the exact nature of this wood spectrum is less clear as many wood traits can vary independently from each other and from wood density (Curtis & Ackerly, 2008). Moreover, the nature of these trait associations may vary from community to community (Jacobsen *et al.*, 2008). Although the adaptive value is often inferred, it is not clear how these wood traits relate to whole-plant performance in the field or to the life history strategies of tree species. Interspecific comparisons are often made by comparing different species measured in different sites (Maherali *et al.*, 2004), thus potentially confounding interspecific and environmental effects.

For closed forests, the shade tolerance of juvenile trees and the stature of reproductive adult trees are considered to be two of the most important life history strategies (Turner, 2001; Poorter *et al.*, 2006). Variation in shade tolerance allows species to partition the horizontal light gradient at the forest floor (Kitajima & Poorter, 2008), whereas differences in adult stature allow species to partition the vertical height gradient in the forest canopy (Poorter *et al.*, 2008a; Kohyama & Takada, 2009). Initial results suggest that fast-growing and shade-intolerant species have large vessels and high hydraulic conductance (Castro-Diez *et al.*, 1998; Tyree *et al.*, 1998; Sack *et al.*, 2005), while tall species have large vessels and a low vessel density (Preston *et al.*, 2006), although the latter has only been observed for woody plants from a Mediterranean-type climate.

In this study we compare quantitative wood traits of 42 coexisting rainforest species. We take advantage of large-scale permanent sample plot data to calculate species-specific growth and survival rates. Wood anatomical traits are related to each other, then to growth and survival rates, and finally to quantitative indices of shade tolerance and adult stature. The rationale behind this approach is that wood traits should affect plant performance and that wood traits together with plant performance shape the life history variation across species. The following three corresponding hypotheses are addressed:
- Wood density increases with fibre cross-sectional area because fibres make up most of the solid wood mass, and wood density decreases with vessel cross-sectional area as more open conduit spaces should lead to less dense material. K_p increases with vessel cross-sectional area, and especially with vessel diameter.
- Diameter growth rate increases with the water transport capacity (vessel cross-sectional area, vessel diameter and K_p), and decreases with the volumetric stem construction cost (wood density) of the species. Survival rate increases with the stem material strength (fibre cross-sectional area and wood density) and carbon storage potential (parenchyma cross-sectional area) of the species.
- Both light-demanding species and tall species have exposed crowns and therefore need high K_p and associated traits to meet their high transpirational demands. At the same time they have stem properties associated with fast growth (high K_p and low wood density). By contrast, both shade-tolerant species and small species have stem properties that are associated with high survival (large fibre cross-sectional area and high wood density).

Materials and Methods

Study site and species

Research was carried out at the tropical, moist, semi-evergreen forest of La Chonta (15°47′S, 62°55′W), Bolivia. The region receives an average annual rainfall of 1580 mm, with a 1-month-long dry period where potential evapotranspiration exceeds precipitation. The forest has an average height of 27 m, basal area of 19.3 m² ha⁻¹, tree density of 367 ha⁻¹, and species richness of 59 ha⁻¹ (all data for trees > 10 cm diameter at breast height (DBH); Peña-Claros *et al.*, 2008).

Forty-two of the most abundant woody species were selected, comprising 71% of all trees > 10 cm DBH in the forest. The species varied in adult stature and regeneration light requirements (see Supporting Information, Table S1). The adult height (H_{max}) of a species is estimated from species-specific regression equations of tree height against DBH. H_{max} was calculated as the predicted height value for the DBH of the third-thickest tree encountered in the per-

manant sample plots (Poorter *et al.*, 2006). The third-thickest rather than the thickest tree was used, thus avoiding outliers caused by incorrect measurements or rare thick 'champion' trees. In a separate study, Poorter & Kitajima (2007) provided an independent, objective and continuous measure of the regeneration light requirements of the species by analysing for each species the crown exposure in relation to the height of individual trees. To this end, on average 523 individuals (range 16–9064) per species were measured over their whole size range for their height and crown exposure (CE) (Dawkins & Field, 1978). The CE has the following values: 1, tree does not receive any direct light; 2, it receives lateral light; 3, it receives overhead light on 10–90% of the crown; 4, it receives full overhead light on > 90% of the crown; 5, it has an emergent crown. The CE can be measured repeatedly (mean difference between two independent observers is 0.1 ± 0.01 SE), and there is a good relation between CE and both canopy openness and incident radiation (Keeling & Phillips, 2007). For each species the CE was related to tree height, using a multinomial regression analysis (cf. Poorter *et al.*, 2005). Using the regression equation, the average population-level CE at a standardized height of 2 m (juvenile crown exposure, CE_{juv}) was calculated. Similar-sized individuals of the same species can be found under a wide range of CEs, but what counts from an evolutionary point of view is the average population-level CE of the species (Poorter *et al.*, 2005). The CE_{juv} (or regeneration light requirements) is the inverse of shade tolerance, and these two expressions will be used interchangeably in this paper.

Data collection

Wood samples were collected at the onset of the rainy season in October 2005, for three individuals per species. Most trees sampled were between 10 and 46 cm DBH, except for the three smallest species (*Erythrochiton fallax*, *Picramnia selowii*, *Triplaris americana*) that do not, or hardly, attain 10 cm DBH, for which the thickest individuals were sampled, and the emergent *Ceiba pentandra* for which no small individuals were found. Using a chisel, two samples (1 × 3 × 3 cm) per tree were taken at 0.5–1.5 m height, including cambium and recently formed wood layers. For one sample per tree, the fresh mass was determined and wood volume was measured using the water displacement method, after which the sample was oven-dried for at least 48 h at 70°C and weighed. Wood density (in g cm^{-3}) was determined as wood dry mass over wood fresh volume. The wood water content (WC, in %) was calculated as $100(1 - (\text{dry mass/fresh mass}))$, and is an indicator of water capacitance. The companion sample was stored in a refrigerator for further analysis of wood anatomical traits.

Wood samples were machine-polished with a Knobber GD 251 sanding machine, utilizing sand paper with 400 and 500 grit. This gave satisfactory results for medium-density wood samples. Surfaces of samples of either very high or very low wood density required additional improvement by boiling and microtome cutting. One sample per species was photographed using a Leica DFC 320 digital camera connected to a Leica MZ 125 microscope. Magnification ranged from ×35 to ×60. These photographs were manually colour-coded for vessels, fibres and parenchyma using Adobe Photoshop CS software (Adobe Systems Incorporated, San Jose, CA, USA). The image analysis was conducted at the department of crop sciences, Agronomy in the Tropics, University of Göttingen, Germany, using the analySIS Pro 3.2 software program (Soft Imaging System GmbH, Münster, Germany). Image analysis on each sample was conducted for the whole wood sample and the last two or three growth rings. Samples were analysed for percentage cross-sectional area occupied by vessel (axial and radial) parenchyma and fibres on the base of colour thresholds. In addition, the area of all individual vessels, vessel density per mm^2 and nearest neighbour distance between vessels (Dist) were measured. The latter variable gives a first indication as to whether vessels are clustered or not. Trait values for the whole sample and the ring measurements were strongly correlated across species, and for further data analyses the whole sample was used.

Potential hydraulic conductivity (K_p) was calculated according to the Hagen–Poiseuille law (Sterck *et al.*, 2008):

$$K_p = (\pi \rho_w / 128 \eta) \times \text{VD} \times D_h^4, \qquad \text{Eqn 1}$$

where K_p is the potential specific stem conductivity (in kg m MPa^{-1} s^{-1}), η is the viscosity of water at 20°C (1.002×10^{-3} Pa s at 20°C), ρ_w is the density of water at 20°C (998.2 kg m^{-3} at 20°C), VD is the vessel density and D_h is the hydraulically weighted vessel diameter (in m). Since vessels are not exactly circular, the diameter of each vessel was calculated as the mean of the minimum and maximum diameters. The average D_h was calculated as (Sterck *et al.*, 2008):

$$D_h = \left[(1/n) \sum_{i=1}^{n} d^4 \right]^{1/4} \qquad \text{Eqn 2}$$

K_p is higher than the true conductivity because the resistance of the vessel perforation plates and pit apertures (Sperry *et al.*, 2005, 2006), and cavitated vessels are not taken into account. Here we assume that those additional resistances will not significantly alter the observed species ranking, and that K_s scales positively with K_p.

Growth and survival rates

Species-specific, population-level growth and survival rates were calculated using permanent sample plot data from the

Instituto Boliviano de Investigación Forestal (IBIF). In La Chonta a long-term silvicultural research programme (LTSRP) is under way in which one of four treatments (control, normal logging, light silviculture and high silviculture) are applied to 12 replicate plots of 27 ha each, using a randomized block design (see Peña-Claros *et al.* (2008) for more detailed information on logging intensities and silvicultural treatments applied). Trees were mapped, tagged, identified and measured for their DBH in a nested design (trees > 40 cm DBH in an area totalling 324 ha, trees 20–40 cm DBH in 160 ha, and trees 10–20 cm DBH in 48 ha), after which the treatments were applied. Trees were monitored for their survival and DBH after 1, 2, 4 and 6 yr. New recruits were measured at each census period as well.

Interspecific comparisons of growth rates might be hampered if growth is size-dependent and if size distributions vary among species. To reduce these size-dependent effects, the diameter growth rates were calculated for all species in a similar, limited diameter range between 10 and 50 cm DBH. 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, in cm yr^{-1}). All trees were included that had at least two DBH measurements (including new recruits), and that did not have measurement problems owing to buttresses or lianas. Average growth and survival rates were calculated per species, combining trees from all treatments to have as large a number of replicates as possible. Pooling growth data for different treatments did not confound the results, as species-specific growth rates were highly correlated across treatments. No growth data were obtained for *Erythrochiton fallax*, *Picramnia selowii* (too small) or *Triplaris americana* (too few individuals). The median number of trees per species for calculation of the growth rates was 246 (range 11–8747). Annual mortality rates (MR) of species were calculated as ($\log_e N_0 - \log_e N_t$) / time, where N_0 and N_t are the number of trees at the beginning and the end of the monitoring period, respectively, and time refers to the number of years between the first and last census (5.93 yr). Only those trees were included that were present at the start of the experiment and that did not die as a result of logging or the application of silvicultural treatments. Trees that were not found again were considered to be dead. All trees > 10 cm DBH were included in this analysis, as MR varies little with tree diameter for trees > 5 cm DBH (Clark & Clark, 1992). Annual survival rates (SR, in % yr^{-1}) were calculated as $100 \times e^{-MR \times 1}$.

Analyses

A principal-component analysis (PCA) was done to evaluate how wood traits were associated among each other. In this way it was established whether, for example, average and maximum vessel diameters (which are commonly measured) are also good indicators for the D_h. After having confirmed the strength of these relationships with the PCA, subsequent analyses were done with the main traits of interest only. In this and other statistical analyses, the traits were $\log_{10}$-transformed if necessary, to enhance normality and homoscedasticity. With a (multiple) regression analysis, wood density was related to parenchyma, vessel and fibre cross-sectional area. Potential hydraulic conductivity (K_p) was related to the vessel cross-sectional area, vessel density and D_h to evaluate which of these components are the strongest determinants of the water transport capacity of trees. Wood traits were related to species performance (diameter growth rate, survival rate) and life history traits (CE_{juv}, H_{max}) with a Pearson correlation and phylogenetic correlation, using species as data points. A correlation analysis rather than a regression analysis was used, as this allowed direct comparison of the sign and the strength of the cross-species and the phylogenetic correlations. Evolutionary correlations were also calculated using phylogenetically independent contrasts, to evaluate whether the observed trait associations are the result of repeated evolutionary divergences. In this analysis, each branching divergence in the phylogenetic tree contributes one data point. A phylogenetic tree was made using the program Phylomatic (Webb & Donoghue, 2005) based on the maximum resolved angiosperm phylogeny (tree R20031202). If one genus was missing from the megatree, then for that family the genera were included as polytomies (i.e. all genera branch from the same node), and species were always included as polytomies within a genus. Because of the incompletely resolved phylogenetic tree with polytomies, the N for the phylogenetic contrast was generally lower ($N = 32–34$) than for the regular cross-species analysis ($N = 38–42$). Phylogenetic correlations were calculated using the 'analysis of traits' module of Phylocom 4.0.1b (Webb *et al.*, 2008). Phylogenetic independent contrasts were calculated as the difference in mean trait values for the two nodes (or two species) descending from a node. Phylogenetic branch lengths were set to 1 and polytomies were resolved to provide one contrast (see Webb *et al.* (2008) for further details).

Results

### Associations amongst wood traits

Wood traits varied substantially across the 42 co-occurring species (Table S1, Fig. 1): wood density varied 2.7-fold (0.28–0.78 g cm^{-3}), fibre cross-sectional area varied 2.8-fold (26–74%), parenchyma cross-sectional area varied 4.8-fold (13–64%), vessel cross-sectional area varied 8.6-fold (3–23%), vessel density varied 509-fold (0.5–270 cm^{-2}), D_h varied 14-fold (0.03–0.46 mm), and K_p varied 1050-fold (1.2–1299 kg m^{-1} s^{-1} MPa^{-1}). None of the tissue fractions was significantly related to wood density (Fig. 2).
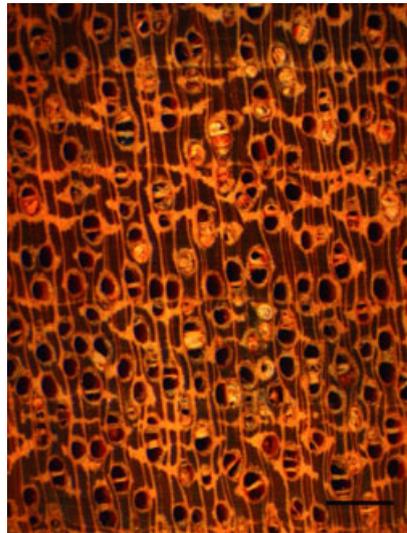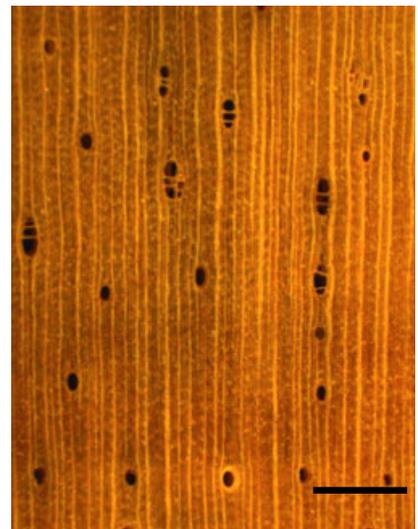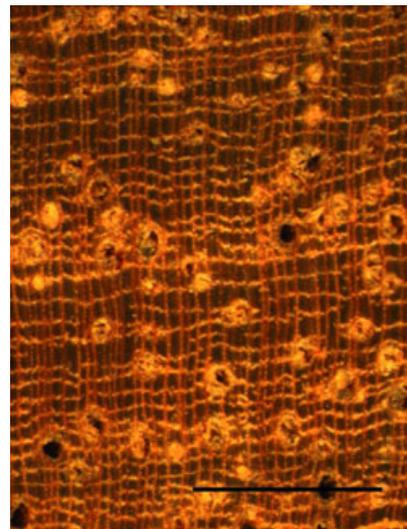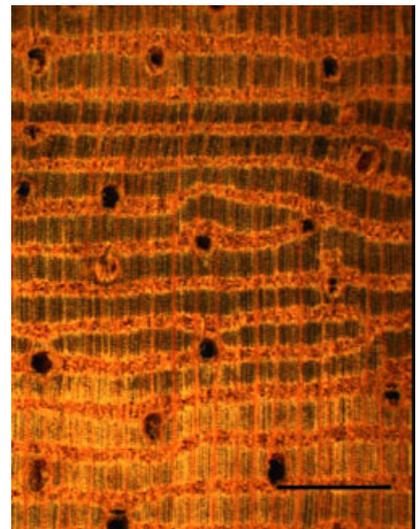
Maclura tinctoria

Aspidosperma rigidum
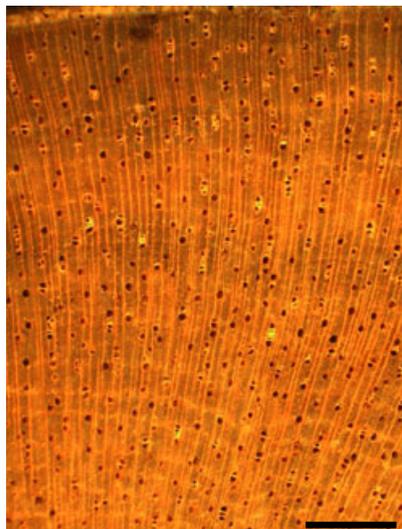
Triplaris americana

Hura crepitans

Hirtella triandra

Ficus boliviana

Fig. 1 Examples of wood anatomy of six rainforest tree species: *Maclura tinctoria* (with high wood density, wide vessels and thick fibre walls), *Aspidosperma rigidum* (with high wood density and high vessel density but narrow vessels), *Triplaris americana* (with low wood density, low vessel density and thin fibre walls), *Hura crepitans* (with low wood density and low vessel density), *Hirtella triandra* (with high wood density, wide vessels and thick fibre walls, and *Ficus boliviana* (with average wood density, wide vessels and low vessel density). Bars, 1 mm.
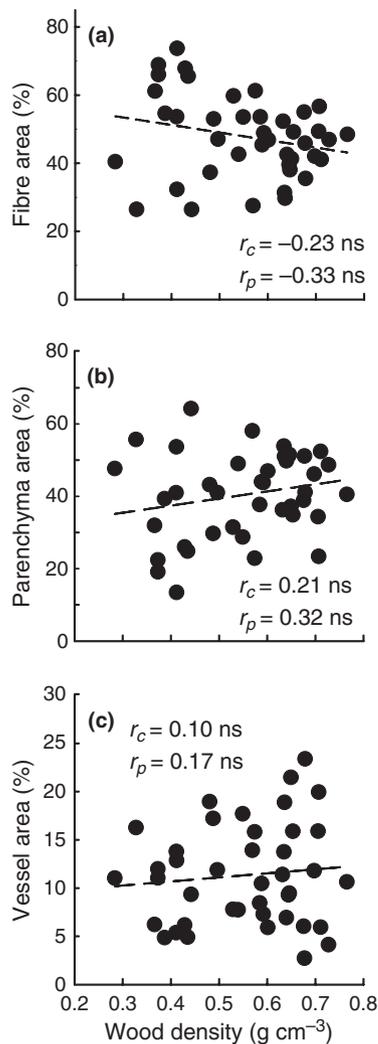
Fig. 2 Relationship between wood density and its underlying anatomical components for rainforest tree species (n = 42). (a) Fibre cross-sectional area; (b) parenchyma cross-sectional area; and (c) vessel cross-sectional area. Regression lines, Pearson cross-species correlation (r_c), phylogenetic correlation (r_p) and significance levels are shown. ns, $P > 0.05$.

Fig. 3 Relationship between potential hydraulic conductance (K_p) and its underlying anatomical components for rainforest tree species (n = 42). (a) Vessel cross-sectional area (VCA); (b) vessel density; (c) hydraulically weighted vessel diameter. Regression lines, Pearson cross-species correlation (r_c), phylogenetic correlation (r_p) and significance levels are shown. ns, $P > 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Potential hydraulic conductivity K_p was not significantly related to vessel cross-sectional area; it was positively related to D_h and negatively related to vessel density (Fig. 3). This negative relationship between K_p and vessel density is surprising, as vessel density should have a positive effect on K_p (Eqn 1). The reason for this counterintuitive result is the very strong trade-off between vessel density and vessel diameter (Fig. 4). When a multiple regression analysis is done, it becomes clear that both parameters did indeed have independent, positive effects on K_p, and that hydraulically weighted vessel diameter was a stronger determinant of K_p (standardized regression slope beta is 1.66, $P < 0.001$) than vessel density (standardized regression slope beta is 0.90, $P < 0.001$) because conductivity scales with the fourth
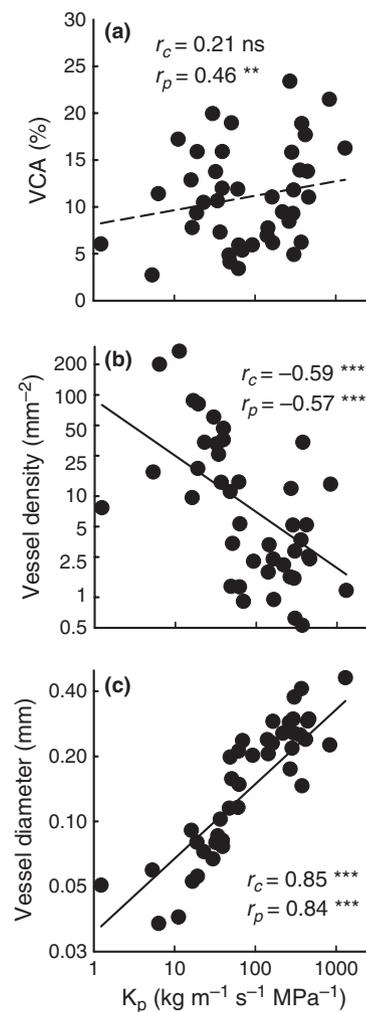
power of vessel radius and only with the first power of vessel density (Eqn 1).

A PCA was done to evaluate how wood traits were associated (Fig. 5). The first axis explained 51% of the variation and shows strong positive loadings for average and maximum vessel diameter, distance to the nearest vessel and K_p, and negative loadings for vessel density and wood density. The second axis explained 21% of the variation and showed a positive loading for parenchyma cross-sectional area and a negative loading for fibre cross-sectional area.

Relationship between wood traits and performance

Growth rate was negatively related to wood and vessel density, and positively related to vessel diameter and K_p (Fig. 6). Surprisingly, growth rate increased with the cross-
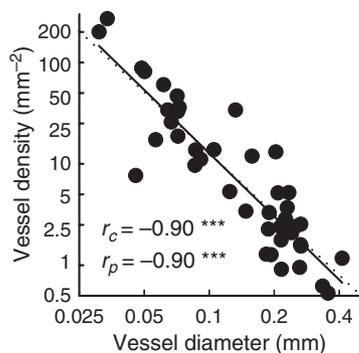
Fig. 4 Trade-off between vessel density and average vessel diameter for 42 rainforest tree species. The dotted isoline indicates the combination of vessel density and vessel diameter that led to the same vessel cross-sectional area (VCA) of 10%. Please note that the average rather than the hydraulically weighted vessel diameter is presented. Regression lines, Pearson cross-species correlation (r_c), phylogenetic correlation (r_p) and significance levels are shown. ***, $P < 0.001$.
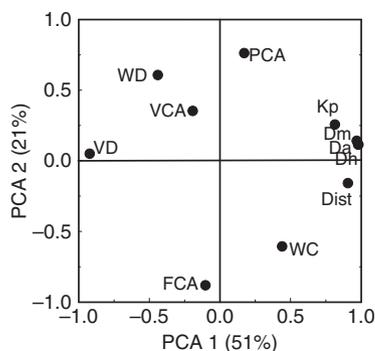

Fig. 5 Principal-component analysis of 11 wood traits of 42 rainforest tree species. PCA, parenchyma cross-sectional area; FCA, fibre cross-sectional area; VCA, vessel cross-sectional area; WD, wood density; WC, water content; VD, vessel density; Dist, distance to nearest vessel; D_a, average vessel diameter; D_m, maximum vessel diameter; D_h, hydraulically weighted vessel diameter; K_p, potential hydraulic conductivity. VD, D_a, D_m, D_h and K_p were $\log_{10}$-transformed before analysis.

sectional area in fibres. Survival rate was only significantly related to wood density, with high-density species showing a higher survival (Table 1).

Relationship between wood traits and life history axes

Juvenile crown exposure (CE_{juv}) and H_{max} showed qualitatively similar relationships with wood traits: the vessel density (Fig. 6e,f) decreased and the vessel diameter increased (Fig. 6h,i) with increased regeneration light requirements and adult stature of the species. Wood density was only significantly (and negatively) related to CE_{juv} (Fig. 6b), and K_p was only significantly and positively related to H_{max} (Fig. 6l). Overall, wood traits were somewhat more strongly related to H_{max} than to CE_{juv}.

Phylogenetic correlations

The phylogenetic analysis showed qualitatively similar results to the cross-species analysis, although quantitatively the correlations sometimes differed in strength. The phylogenetic correlations were significant in two cases, whereas the cross-species correlations were not significant for vessel cross-sectional area vs K_p (Fig. 3a) and wood density vs H_{max} (Fig. 6c). In many cases, both correlations were similar in strength (Figs 2, 3b,c, 4, part of Fig. 6), whereas the cross-species correlations were significant for the relationships between vessel traits and growth rate or CE_{juv} while the phylogenetic correlations were not (Fig 6).

Discussion

The coexisting tree species differed strikingly in their wood anatomical traits. Here we first discuss how wood traits are associated, then the strong implications they have for tree growth and survival, and finally that this wood spectrum is closely related to two important life history axes of variation: the regeneration light requirements and adult stature of the species.

Associations amongst wood traits

It was expected that wood density would increase with fibre cross-sectional area because, of all tissue types, fibres have the thickest cell walls and hence contribute to a large extent to the density of the wood matrix. Wood density was also expected to decrease with vessel cross-sectional area, as more open conduit spaces should lead to less dense material (cf. Preston *et al.*, 2006). Surprisingly, neither straightforward prediction held (Fig. 2a,c). This counterintuitive result can be explained by strong interspecific differences in the density of the fibre tissue. Species that combined a large fibre cross-sectional area with low wood density (such as *Triplaris*, *Hura* and *Trema*) probably have fibre cells with thin walls and large lumina. By contrast, species that combined a low fibre cross-sectional area with high wood density (such as *Aspidosperma, Pouteria nemerosa* and *Terminalia*) probably have fibre cells with thickened walls and small lumina (Fig. 1). Variation in wood density across these 42 sympatrically occurring rainforest tree species might therefore be driven by fibre cell wall thickness, rather than by variation in fibre tissue area. These assumptions agree with observations made of arid fynbos shrub species by Jacobsen *et al.* (2007), showing that wood density increased with the fibre wall thickness and decreased with fibre lumen area.

No significant relationship was found between wood density and vessel cross-sectional area (Fig. 2c), which is contrary to the prediction but in line with the results obtained by Zanne *et al.* (in press) in a global meta-analysis of 3000 angiosperm woody species. The influence of vessel
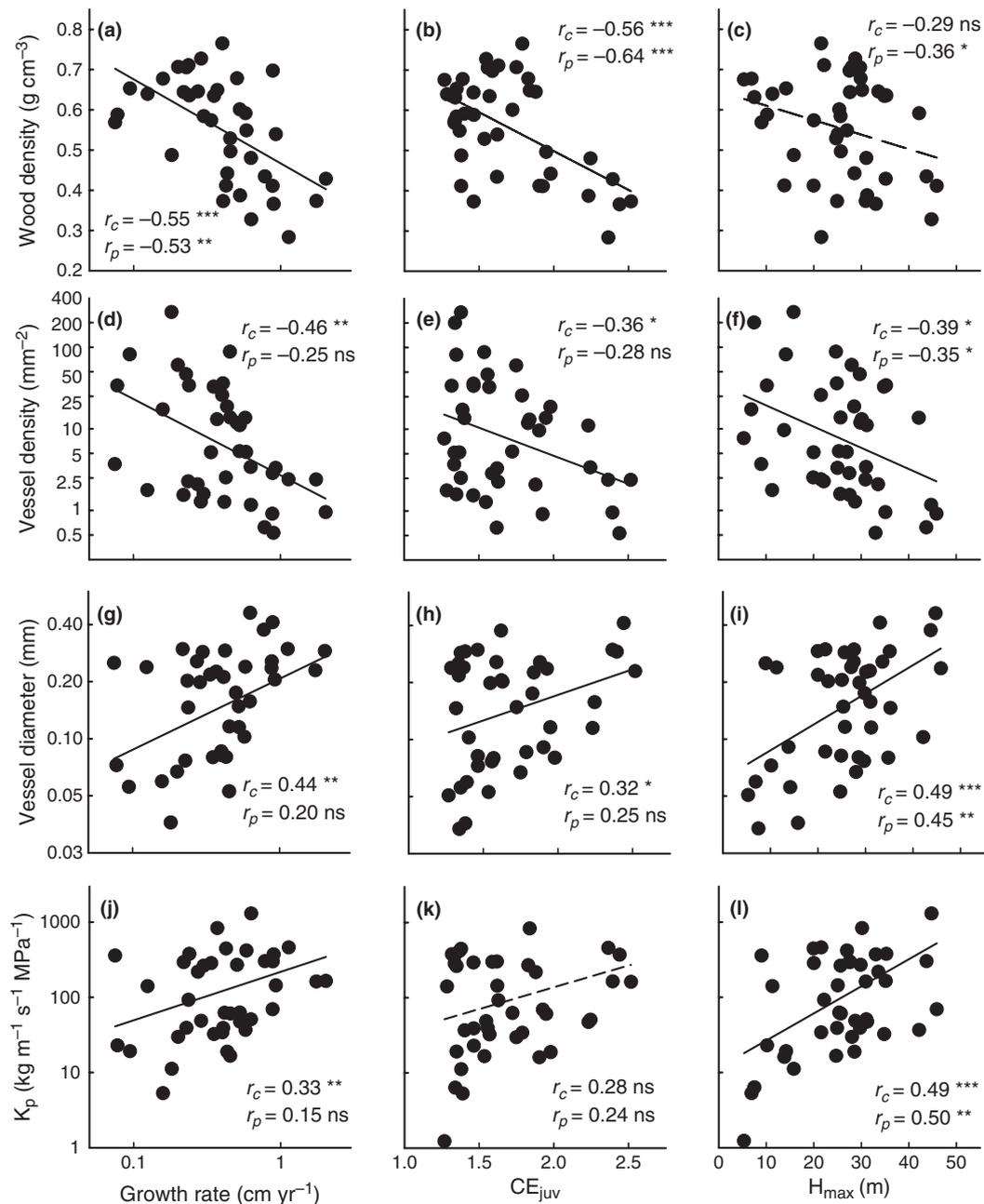
Fig. 6 Relationship between wood traits, diameter growth rate (GR), juvenile crown exposure (CE$_{juv}$) and adult stature (H$_{max}$) of rainforest tree species (*n* = 38–42). (a–c) Wood density; (b–f) vessel density; (g–i) hydraulically weighted vessel diameter; and (j–l) potential hydraulic conductance (K$_p$). Regression lines, Pearson cross-species correlation (r$_c$), phylogenetic correlation (r$_p$) and significance levels are shown. ns, *P* > 0.05; *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001. Phylogenetic correlations are based on 32–34 contrasts.

cross-sectional area on wood density can be expressed as WD = WDNL (100 − VCA), where WDNL is the density of tissue outside vessel lumens (Preston *et al.*, 2006) and VCA is the vessel cross-sectional area. Given the fact that only a small part of the woody tissue is made up of vessels (3–23%), it is likely that the small negative effect of vessel area on wood density is overruled by the large interspecific variation in WDNL. This shows that wood density of

different species is complexly related to cross-sectional area of different tissue types as well as to the morphology of the cells, such as cell wall thickness. Again, the density of fibres (in terms of mass per volume) is important in this respect, because in most species fibres make up the bulk of the woody tissue (26–74% of the cross-sectional area).

It was expected that the hydraulic conductivity would scale positively with the vessel cross-sectional area, as a

Table 1 Pairwise Pearson correlations between wood traits, vital rates (diameter growth rate and survival rate) and life history axes (juvenile crown exposure, adult stature) of rainforest tree species

	WD	FCA	PCA	VCA	VD	D_h	K_p	GR	SR	CE$_{juv}$	H_{max}
Wood density (WD)		−0.33	0.32	0.17	0.22	−0.17	−0.10	**−0.53**	0.33	**−0.64**	**−0.36**
Fibre cross-sectional area (FCA)	−0.23		**−0.90**	**−0.58**	−0.18	−0.12	−0.29	**0.53**	−0.17	0.28	−0.06
Parenchyma cross-sectional area (PCA)	0.21	**−0.91**		0.16	0.10	0.03	0.09	**0.55**	0.19	−0.32	−0.05
Vessel cross-sectional area (VCA)	0.10	−0.30	−0.14		0.32	0.11	**0.46**	0.13	−0.02	0.00	0.17
Vessel density (VD)[1]	0.30	−0.01	−0.16	**0.42**		**−0.90**	**−0.57**	−0.25	−0.20	−0.28	**−0.35**
Vessel diameter (D_h)[1]	**−0.31**	−0.15	0.18	−0.10	**−0.90**		**0.84**	0.20	0.21	0.25	**0.45**
Potential hydraulic conductance (K_p)[1]	−0.24	−0.25	0.15	0.21	**−0.59**	**0.85**		0.15	0.07	0.24	**0.50**
Growth rate (GR)[1]	**−0.55**	**0.32**	−0.27	−0.17	**−0.46**	**0.44**	0.33		−0.07	**0.67**	**0.63**
Survival rate (SR)	**0.40**	−0.20	0.23	−0.07	−0.03	−0.01	−0.12	−0.15		−0.22	**0.51**
Juvenile crown exposure (CE$_{juv}$)	**−0.56**	0.20	−0.17	−0.09	**−0.36**	**0.32**	0.28	**0.68**	−0.26		**0.60**
Adult stature (H_{max})	−0.29	−0.04	0.00	0.03	**−0.39**	**0.49**	**0.49**	**0.64**	**0.40**	**0.43**	

Regular cross-species correlations are shown below the diagonal (n = 38–42) and phylogenetic correlations are shown above the diagonal (n = 32–35). Bold correlation coefficients have a P-value < 0.05, and bold and underlined coefficients have a P-value < 0.01.
[1]$\log_{10}$-transformed before analysis.

larger total conduit area would enable a larger sap flow. From the isoline in Fig. 4, it can be seen that a wide range of vessel densities and vessel diameters result in the same vessel cross-sectional area of 10%. Most of the species fall along the isoline, indicating that they differ only modestly in VCA (3–23%), despite striking differences in average vessel diameter and density. For our study species, this modest interspecific variation in VCA was only significantly related to vessel density but not to average vessel diameter (Table 1), probably because of the substantially larger variation in vessel density (509-fold) compared with vessel diameter (eightfold, Table S1). As VCA is mostly determined by vessel density, whereas K_p is mostly determined by vessel diameter, it becomes clear why VCA and K_p are largely uncoupled (Fig. 3a).

There was a strong trade-off between vessel density and vessel diameter (Fig. 4). For coniferous species, such a trade-off is expected, as they possess only one tissue type (tracheids), and physically either many small conduits or a few large conduits can be packed into the same area. For broadleaved species, such a trade-off is less obvious, since their wood is made up of three tissue types, and vessels make up only a small proportion of the wood (3–23%). In principle there should be ample opportunity for broad-leaved species to make both larger vessels and a greater number of vessels, but apparently this combination is not feasible, perhaps because of biomechanical constraints (cf. Preston *et al.*, 2006). This trade-off has been found in many studies and has been interpreted as a trade-off between hydraulic efficiency and hydraulic safety (Baas, 1986; Sperry *et al.*, 2008) in which species with many small vessels have coassociated traits that tend to reduce the risk of dysfunctional cavitated vessels.

The PCA (Fig. 5) illustrates these trait associations. The first axis shows a positive relationship between K_p and average vessel diameter, on the one hand, and a negative relationship between these traits and the vessel density and

wood density, on the other hand. This first axis therefore reflects the vessel size–number trade-off, that is, the trade-off between hydraulic efficiency and hydraulic safety. Independent of this axis is a second axis that reflects the trade-off between investments in different tissue types, notably the fibre and parenchyma cross-sectional area. Probably the strongest trade-off is between these two components because the complementary tissue type (vessel area) occupies only a small fraction of the cross-sectional wood area. Wood density loads equally well on both axes, which is perhaps the reason why it is a good proxy for many different stem functions.

Relationship between wood traits and species performance

We hypothesized that stem diameter growth rate would increase with the water transport capacity and decrease with the volumetric stem construction cost of the species. In the cross-species analysis, vessel diameter (Fig. 6g) and potential hydraulic conductivity (K_p, Fig. 6j) were positively related to growth, as predicted, because trees possessing wider vessels have larger K_p and more efficient water transport through the stem. The efficient water transport allows for higher stomatal conductance, and hence photosynthetic rates, thus fuelling growth. It has been frequently demonstrated that hydraulics affect photosynthetic carbon gain (Brodribb & Field, 2000; Brodribb *et al.*, 2002; Santiago *et al.*, 2004). A recent study shows that hydraulic conductance of 17 dipterocarp species is positively related to the diameter growth rate of plantation-grown trees (Zhang & Cao, 2009), but to our knowledge it has never been shown that it is also positively related to growth performance of naturally growing plants in the field. An additional advantage of a higher water flow is that a larger leaf area can be supplied with water, and wood properties that facilitate high water flow therefore contribute positively to light

interception, carbon gain and growth. Relationships between vessel traits and growth were significant in the cross-species analysis but not in the phylogenetic analysis. A lesser significance in the phylogenetic analysis might be the result of an incompletely resolved phylogenetic tree and a lower number of contrasts, but the fact that the phylogenetic correlation was also smaller suggests that these vessel trait–growth relationships are less consistent from an evolutionary point of view.

Wood density was negatively related to growth (Fig. 6a), as predicted, probably because low-density wood is cheaper to construct and allows for more rapid growth in stem dimensions. Similar results have been found in various field studies concerning rainforest saplings (Muller-Landau, 2004; Poorter, 2008) and trees (summarized in Ter Steege, 2003; King *et al.*, 2005; Poorter *et al.*, 2008b). Wood density may also have an indirect effect on growth, as species with low-density wood have large vessels and tend to have high K_p (Table 1), thus stimulating carbon gain (Santiago *et al.*, 2004; Meinzer *et al.*, 2009).

We hypothesized that the survival rate would increase with the stem material strength and carbohydrate storage potential of the species. Wood density was indeed positively related to survival rate ($r = 0.40$, Table 1, cf. Kitajima, 1994; Muller-Landau, 2004; Poorter, 2008; Poorter *et al.*, 2008b) supporting the idea that species with high wood density have higher mechanical strength and are therefore more resistant to damage from wind (Putz *et al.*, 1983; Curran *et al.*, 2008), falling debris (dense wood is stiff and breaks less easily; Van Gelder *et al.*, 2006) or pathogen attack (Augspurger & Kelly, 1984; Loehle, 1988). Dense-wooded species are also better at reducing the spread of decay once they are damaged (Romero & Bolker, 2008). Fibre cross-sectional area was not related to survival, probably because species with the largest fibre cross-sectional area may have fibres with small fibre wall thickness, and it is the ratio of fibre wall thickness to fibre lumen area, in particular, that determines fibre strength (Hacke *et al.*, 2001). The parenchyma cross-sectional area was not related to survival (Table 1), contrary to the prediction. It was expected that a higher parenchyma cross-sectional area would enable species to store more carbohydrates that can be used to overcome stress or damage (Kobe, 1997; Myers & Kitajima, 2007). Several factors can explain the absence of such a relationship: the carbohydrate storage potential is determined to a greater extent by total stem volume than by the stem fraction of storage tissue; roots and bark may be more important storage organs for carbon than stems (Canham *et al.*, 1999); the presence of living fibres in some of the studies species may not allow for a strict separation into storage and supporting tissue, as living fibres and parenchyma provide both functions; and/or the carbohydrate pool size may be a limiting factor for the survival of small seedlings, but not for the survival of large trees.

Relationship between wood traits and life history axes

We hypothesized that light-demanding/tall species would have stem properties associated with high water transport capacity and fast growth, whereas shade-tolerant/small species would have stem properties associated with high survival. Light-demanding and tall species were indeed characterized by fast growth (Table 1) and had stem traits that facilitate fast growth, such as high vessel diameter (both groups), high K_p (tall species) and low wood density (light-demanding species, Fig. 6). Light-demanding species regenerate in gaps and should have high growth rates to attain a position in the canopy before the gap is closed, whereas tall species should grow quickly to rapidly attain their large reproductive size (Thomas, 1996). Both light-demanding and tall species should also have a high K_p to meet the high transpirational demands that go along with their exposed, sun-lit crowns. Although light-demanding and tall species have much in common, they do differ in some crucial aspects as well. For example, tall species suffer from larger vapour pressure deficits high up in the exposed canopy compared with smaller light-demanding pioneer species growing in the lower forest strata in gaps. In addition, they have considerably longer hydraulic path lengths. Consequently, tall canopy species should experience more drought stress than light-demanding species and, everything else being equal, they should also face a higher risk of cavitation, unless this is compensated for by a considerably larger rooting volume of the canopy species or more narrowly tapering vessels up in the crown. A logical corollary would be that hydraulic traits are more closely associated with H_{max} than with $CE_{juv.}$ Traits related to hydraulic conductance, such as vessel diameter and K_p, indeed showed a stronger relation with H_{max} than with CE_{juv}, especially for the phylogenetic correlations. Tall species could also increase their vessel density and cross-sectional parenchyma, thus guaranteeing hydraulic safety and replenishment of embolized vessels. However, parenchyma cross-sectional area was not related to H_{max}, and vessel density was even negatively related to H_{max}, contrary to the prediction. Similar relationships with H_{max} have been observed in Californian flora, where large trees have wider vessels and lower vessel density compared with shrubs (Carlquist & Hoekman, 1985; Preston *et al.*, 2006). Preston *et al.* (2006) suggest that tall species have a low vessel density to compensate for their high vessel diameter, which would allow them to maintain sufficient wood density for mechanical safety and defence. In our dataset, vessel density and wood density were indeed positively correlated, although this was at the edge of significance.

We hypothesized that shade-tolerant/small species should possess stem traits that enhance survival. Wood density was the only stem trait that was (positively) associated with survival, and shade-tolerant species were indeed characterized by a high wood density. For adult stature, the pat-

terns were less clear, possibly because shade-tolerant and light-demanding pioneer species show opposite relationships between wood density and H_{max} (cf. Falster & Westoby, 2005; Van Gelder *et al.*, 2006).

Plant growth and survival depend on a whole suite of coordinated stem, leaf and root traits that together shape the life history strategy of the species (Lambers & Poorter, 1992; Reich *et al.*, 2003; Cavender-Bares *et al.*, 2004), but relatively little is known about the role of wood anatomical traits. This study shows that sympatrically occurring tree species differ strikingly in their wood anatomical traits. The species show two orthogonal axes of trait variation: a primary axis related to the vessel size–number trade-off (reflecting investment in hydraulic conductance vs hydraulic safety) and a secondary axis related to investment in different tissue types. The ecological significance of this secondary axis is still unclear. Vessel traits affect growth, and wood density affects growth and survival in the field. Vessel traits and wood density are therefore important for species performance and closely related to the life history strategies of tropical tree species.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Overview of the 42 rainforest tree species included, their juvenile crown exposure (CE_{juv}), adult stature (H_{max}) and wood traits.

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