

Strong radial variation in wood density follows a uniform pattern in two neotropical rain forests

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Summary

1. Wood density (WD) affects plant biomechanics, drought and decay resistance. As a consequence, WD is an important functional trait related to plant demography and ecosystem processes, which is also used to estimate tree biomass. Radial variation in WD (changes from the centre of the stem to the cambium) affects the strength of the entire stem, but also reflects any changes in wood functional properties that might occur during a tree's lifetime.
2. To understand how WD and radial WD gradients, which were defined as the slope of the relationship between WD and distance to the centre, are related to demographic traits of species, we investigated WD in 335 tree species from a Panamanian moist forest and 501 species from an Ecuadorian rain forest and radial density gradients in 118 and 186 species, respectively, and compared WD with tree growth, mortality and size.
3. WD was negatively related to tree growth and mortality. WD tended to increase towards the outside in trees with low initial density and to decrease towards the outside in trees with high initial density. Radial WD gradients were largely unrelated to tree size and demographic traits, but some families had higher or lower WD gradients at a given inner WD.
4. Inner WD was by far the best predictor of radial WD gradients ($r^2 = 0.39$ for Panama and 0.45 for Ecuador) and this relationship was indistinguishable between the two rain forests. This suggests a broadly uniform function of WD variation, likely responding to mechanical requirements during ontogeny. We discuss the factors potentially driving radial increases or decreases in WD and suggest ways to elucidate the relative importance of tree mechanics, hydraulic safety or decay resistance.
5. We also discuss that not accounting for radial WD gradients may result in substantial errors in WD of the whole stem and consequently biomass estimates, and recommend sampling density gradients when obtaining density data from tree cores.

Key-words: biomass estimate, biomechanics, phylogenetic signal, radial wood density gradient, tropical rain forest, wood function

Introduction

Wood density (WD) is defined as wood dry mass divided by fresh volume and is widely used as a key functional trait (McGill *et al.* 2006; Westoby and Wright 2006; Chave *et al.* 2009). The primary functions of wood are mechanical support, water transport, defence against pests, and storage of water, carbohydrates and nutrients (Chave *et al.* 2009). WD is correlated with many of these functions, with tissue strength and decay and drought resistance increasing

with WD, while water storage or capacitance decreasing with WD (Hacke *et al.* 2001; Pratt *et al.* 2007; Chave *et al.* 2009; Niklas & Spatz 2010). For trees growing in closed forests, environmental conditions change drastically with ontogeny from the seedling to adult stages, and the functional demands on wood and wood traits including WD should change accordingly. Because wood is largely composed of dead cell walls that change little after having been formed, ontogenetic changes in WD will leave a lasting imprint that is seen in a radial WD gradient in adult trees.

Woodcock and Shier (2002) suggest that pioneers produce low-density wood and maximize diameter and

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height growth at times of abundant resources (light) when the race to the canopy is intense. Upon reaching the canopy, rapid growth is less important, wind stress increases and a pioneer might invest in higher-density wood for biomechanical reasons – the strength of the outermost layer makes a disproportionately large contribution to the overall strength of a cylindrical stem. In contrast in shade-tolerant species, height growth is often inhibited by overtopping trees, and juveniles grow slowly and produce well-defended, high-density wood able to withstand branch falls from above and prolonged exposure to pests in the humid understorey. Upon reaching the canopy, a previously suppressed shade-tolerant tree might produce lower-density wood to increase the second moment of area of the trunk and resistance to bending stresses that could lead to mechanical failure (Woodcock & Shier 2002).

Not only mechanical requirements can change during ontogeny. For instance, the inner wood often has lower hydraulic conductivity and may differ in the vulnerability to embolism (Lachenbruch, Moore & Evans 2011). Embolism resistance increases with WD (Markensteijn *et al.* 2011; Sterck *et al.* 2012). Although the vessel lumina that transport water cannot contribute to mechanical support, there appears to be little trade-off between hydraulic conductance and WD (Poorter *et al.* 2009). Interestingly, the radial variation of many wood traits, including WD, is strongly related to tree age rather than tree size, suggesting a direct developmental control related to cambial age (Lachenbruch, Moore & Evans 2011).

To understand what affects WD and radial WD gradients, we evaluate radial WD gradients for 304 species from two old-growth tropical forests in central Panama and Amazonian Ecuador and mean WD for 825 species. We then use these data to evaluate relationships between WD in the stem centre and radial gradients in WD for species-level data and phylogenetically independent contrasts (PICs) and also test whether this relationship differs between large families. PICs test whether correlations found result from phylogenetic relatedness between species or had developed independently. We also tested whether radial gradients in WD are related to the gradient from light-demanding to coexisting shade-tolerant species by comparing WD and WD gradients to growth and mortality rates, which are known to scale along the light-demanding/shade-tolerant gradient.

Between and within-species variation in WD is also important to calculate above-ground biomass (AGB) and carbon storage (Fearnside 1997; Nogueira, Fearnside & Nelson 2008). For example, WD explained 45.4% and 29.7% of the variation in AGB in Brazilian forest plots, with basal area explaining most of the remainder (Baker *et al.* 2004). If WD varies within the tree, this variation needs to be understood to scale from wood samples to the mean density of the entire stem. We will therefore explore how the observed radial WD gradients might influence biomass estimates.

Materials and methods

The study sites were Barro Colorado Island (BCI), Panama and the Estación Científica Yasuni, Ecuador. At BCI, air temperatures average 27.4 °C, annual rainfall averages 2600 mm, and there is a 4-month dry season during which monthly rainfall averages <100 mm. A 50-ha forest plot was established in 1982 and was remeasured in 1985 and every 5 years since (Hubbell & Foster 1992; Condit *et al.* 2006). At Yasuni, air temperatures average 24.8 °C, annual rainfall averages 3100 mm and the minimum mean monthly rainfall is 152 mm. A 25-ha plot was censused in 1995, 2002 and 2007 (Valencia *et al.* 2009). Trees were sampled within 2 km but outside the Yasuni 25-ha plot and within 15 km but outside BCI.

To measure wood density, we collected wood samples with standard 5-mm increment borers. One core was taken to the centre of each tree. Starting at the cambium, we split each core into 5-cm segments, but segments were sometimes smaller when the core broke during sampling. We measured the radial position, length, fresh volume and dry mass of each segment and used the radial position along the core and the diameter of the stem to calculate the distance (D) from the centre of the stem to the centre of each segment. Cores were placed in sealed plastic straws inside plastic bags with a slightly moistened paper towel and held on ice until fresh volume was determined within 24 h of collection. Fresh volume (to 0.1 mm³) was determined by the water displacement method, dry mass (0.1 mg) was measured after drying to constant mass at 100 °C, and WD was defined as dry mass divided by fresh volume. We calculated WD for each segment and then calculated mean WD over segments weighted by the area of the annulus represented by each segment assuming a cylindrical trunk. We calculated mean WD for each individual and mean WD for each of 335 species from Panama and 501 from Ecuador with a minimum of three individuals sampled. These species represent c. 90% and 50% of stems in the BCI and Yasuni plots, respectively. We calculated radial WD gradients for the 118 and 186 species from Panama and Ecuador, respectively, which also had three or more individuals with three or more radial segments for each core.

DATA ANALYSIS

As WD may not change linearly with D, we first calculated for each species a linear correlation between WD and the distance D to the centre of the stem and a logarithmic correlation [ln(WD) vs. D]. The mean r^2 values were very similar for correlations with WD and ln(WD) (0.210 vs. 0.207 for BCI, 0.240 vs. 0.244 for Yasuni) and we thus proceeded with the simplest model using a linear WD–D relationships of the form $WD = WD_{ctr} + WD_{rad} \times D$, with WD_{ctr} the WD in the centre of the stem, WD_{rad} , the radial WD gradient being the change of WD with increasing distance (D) from the stem centre. Regressions were calculated by pooling data from three to five trees per species. Two species with extreme density gradients were excluded because the extremely hard wood of *Tabebuia guayacan* precluded taking cores to the centre of the tree and because the four individual trees sampled for *Annona spraguei* produced extremely different regressions.

We tested whether in species with high inner WD, WD tends to increase towards the bark, and in trees with high inner WD, WD decreases by calculating a linear correlation between WD_{ctr} and WD_{rad} from the species-wise regressions. A correlation between WD_{ctr} and WD_{rad} could result from random variation alone, because a short sequence of random values, as used in the species-wise regressions, is likely to have a negative slope if the initial value is large and vice versa. We therefore conducted a randomization test to evaluate the significance of the observed correlation between WD_{ctr} and WD_{rad} . We randomized the position of segments (i.e. assigned density values to a random selection of

distance values in the WD-D regression), calculated WD_{ctr} and WD_{rad} from linear regressions for these randomized values and the r^2 of the $WD_{ctr} : WD_{rad}$ correlation. This was repeated 1000 times to obtain the 95% confidence interval (as the 0.025 and 0.975 quantile) of the r^2 that might result from a random distribution alone.

We also evaluated relationships between WD_{ctr} , WD_{rad} and maximum adult size and growth and mortality rates. We measured the heights and diameters at breast height (DBH) of the six largest (by DBH) individuals of each species in the BCI 50-ha plot in 2007. Relative growth rates (RGR) and mortality of saplings (trees 10–49 mm DBH) were obtained from repeated censuses of the forest dynamics plots at BCI and Yasuni (see Wright *et al.* 2010 for details) for species with more than 49 observations. We used 95th percentile values of RGR (RGR_{95}) and calculated mortality rates for the 25% of saplings of each species with the smallest RGR in the previous census interval (M_{25}). We chose RGR_{95} and M_{25} to represent growth and mortality rates because these values more closely reflect potential species differences than do mean or median values over all individuals. RGR_{95} and M_{25} data were log-transformed for statistical tests. We evaluated the contribution of genus-, family- and order-level variation to mean WD and WD_{rad} through variance partitioning of a nested ANOVA (genus nested within family nested within order) using the 'varcomp' function of R package 'ape' with data from BCI and Yasuni pooled.

We repeated these species-level analyses using phylogenetically independent contrasts (PICs, Felsenstein 1985). We used two different phylogenetic trees for BCI. A barcode phylogeny based on three plastid loci is available for 281 woody species from the BCI 50-ha plot (Kress *et al.* 2009). This barcode phylogeny resolves 97.5% of all nodes compared to just 48.4% using a tree based on the angiosperm phylogeny (Kress *et al.* 2009). PICs from the barcode tree were calculated only for the regression between WD_{ctr} and WD_{rad} , but not for demographic traits because here too few barcode species also had the 50 or more individuals necessary to estimate RGR_{95} and M_{25} . In addition, only half of our Panama species are included in the BCI barcode phylogeny and no barcode phylogeny exists for Yasuni. For these reasons, we also constructed a phylogenetic tree using Phylocom 4.1 (<http://phylodiversity.net/phylocom/>) based on the APG3-derived megatree. Rather than setting branch lengths uniformly to 1, we used estimated ages of angiosperm nodes (Wikström, Savolainen & Chase 2001) and fixed other nodes by setting branch lengths evenly between the dated nodes using Phylocom's function 'bladj'. The phylogenetic tree based on the barcode phylogeny for BCI was transformed with Pagel's λ because several terminal branch lengths equalled zero (Pagel 1999; λ set to 0.95). This transformation makes all terminal branch lengths larger than zero without changing the relative lengths of nonterminal branch lengths. Polytomies in the Phylomatic tree were resolved with R function multi2di, which transforms all polytomies into a series of dichotomies, PICs were calculated with the R package Picante, and PIC regressions were forced through the origin as is standard in PIC analysis (Garland, Harvey & Ives 1992). Statistics were calculated with R 2.12.1 (<http://cran.r-project.org>).

Results

The species-level mean wood density was slightly lower for 334 species from Panama (0.570 ± 0.146 SD) than for 501 species from Yasuni (0.597 ± 0.127 , t -test $P = 0.007$, Fig. 1a,d). Mean WD of the species used to analyse WD_{rad} was 0.531 ± 0.146 , $n = 118$ for Panama and 0.526 ± 0.114 , $n = 186$ for Yasuni. This is lower than the above mean WD for all species because the analysis of

WD_{rad} excluded smaller trees that did not yield a core >10 cm length and there was a small but significant negative correlation between mean WD and DBH (Pearson $r^2 = 0.02$, $P < 0.001$). The mean wood density of the outermost segment (WD_{outer}) averaged $0.539 (\pm 0.134)$ and $0.517 (\pm 0.106)$ for 118 and 186 species from Panama and Yasuni, respectively (Fig. 1b,e). The mean WD of segments within 5 cm of the centre of each tree (WD_{inner}) averaged $0.494 (\pm 0.160)$ and $0.481 (\pm 0.136)$ for Panama and Yasuni, respectively (Fig. 1c,f). WD_{inner} and WD_{outer} did not differ between Panama and Yasuni ($P = 0.46$ and 0.10). WD_{inner} was nearly identical to the WD_{ctr} , the intercept of the linear regression between WD and D (the distance to the centre). The mean difference between WD_{inner} and WD_{ctr} for species from Panama was -0.012 and for Yasuni 0.001 , with WD_{inner} and WD_{ctr} highly correlated ($r^2 = 0.94$ for Panama and Yasuni). Differences between mean WD, WD_{inner} and WD_{outer} were highly significant ($P < 0.001$, paired t -tests), with species pooled over sites.

Radial gradients in wood density (WD_{rad}) differed significantly (t -test $P = 0.027$) between Panama (0.161 ± 0.654 g cm⁻³ m⁻¹) and Yasuni (0.331 ± 0.649 g cm⁻³ m⁻¹). About half of the species had density gradients between -0.5 and 0.5 in both forests. However, 14% of Panamanian species and 16% of Yasuni species had density gradients < -1 or > 1 (Fig. 2). A WD_{rad} of 1 g cm⁻³ m⁻¹ is substantial and means a 30-cm DBH tree with WD_{inner} equal to 0.5 would have WD_{outer} equal to 0.8, an increase of 60%. Positive density gradients (i.e. density increasing with distance from the centre) were more common than negative ones. Eight species from Panama and nine from Yasuni had significant ($P < 0.05$) negative and 21 and 51 species had significant positive density gradients (Fig. 2).

The species-level relationships between the WD_{ctr} and the WD_{rad} were significantly negative (Panama: $P < 0.001$, $r^2 = 0.387$, Yasuni: $P < 0.001$, $r^2 = 0.451$, Fig. 3). These r^2 values lie well outside the 95% confidence intervals for randomized relationships between WD and D (0.002–0.100 for Panama and 0.040–0.190 for Yasuni). The negative relationships between WD_{ctr} and WD_{rad} ensured that species-level values of WD_{outer} were more similar than WD_{inner} . Consequently, interspecific variation was significantly larger for WD_{inner} than for WD_{outer} (F -test, Panama: $F_{2,227} = 1.414$, $P = 0.06$, Fig. 1b,c, Yasuni: $F_{2,357} = 1.636$, $P = 0.001$, Fig. 1e,f).

The PIC relationships between WD_{ctr} and WD_{rad} for the APG3 tree were weaker than the species-level relationship for Yasuni ($r^2 = 0.308$) but stronger for BCI ($r^2 = 0.494$). The strength of the PIC relationships for the barcode phylogeny and APG3 phylogeny was almost identical for Panama ($r^2 = 0.494$ vs. 0.508) even though the APG3 tree includes all 118 species and a large number of polytomies.

In the ANCOVA for site ($WD_{rad} = WD_{ctr} \times \text{site}$), the homogeneity of slopes assumption was met ($P = 0.261$) and there was no effect of site ($P = 0.180$) on WD_{rad} . Thus, the slopes and intercepts of the relationship between WD_{ctr} and WD_{rad} (Fig. 3) were statistically indistinguishable between

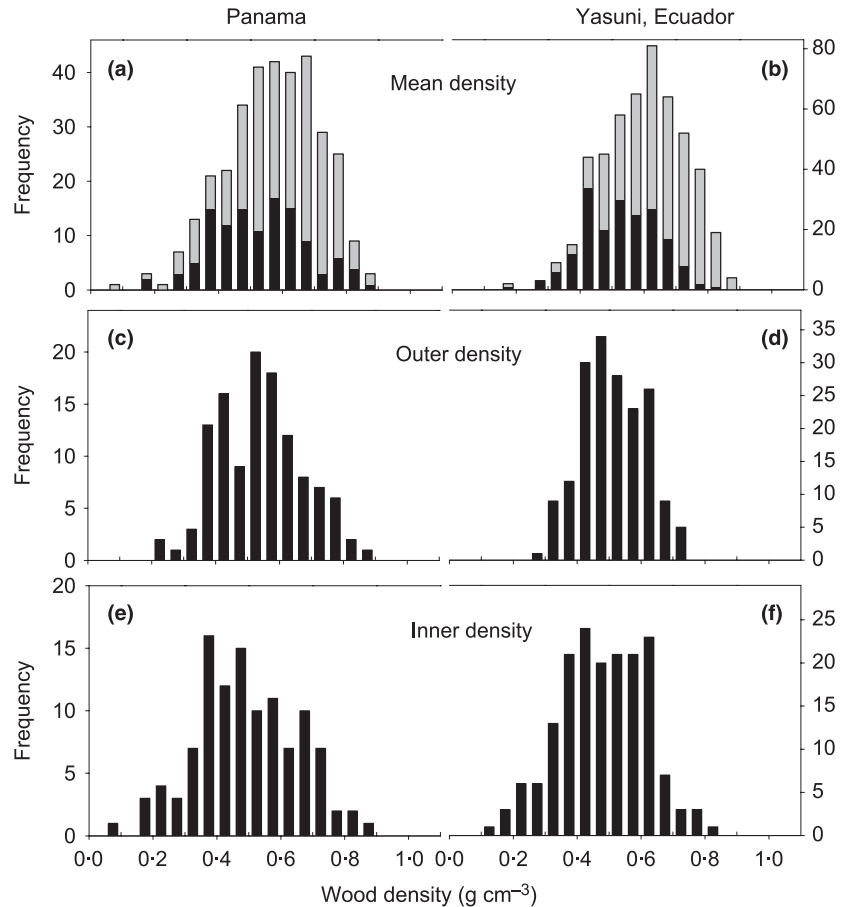


Fig. 1. Wood densities of tree species from tropical wet forests around Barro Colorado Island, Panama, and Yasuni, Ecuador. Values are mean density of all samples per tree (a, b), the density of outermost sample (c, d) and the density of wood samples within 5 cm of the calculated distance to the stem centre (e, f). Substantially more species are included in mean densities because species included in radial variation had to have at least three individuals with three samples per core and a total core length >10 cm. Black bars in (a) and (d) are species included in the other four panels.

Panama and Yasuni. Similar results were obtained for PICs based on the APG3 tree for both sites (site \times WD_{ctr} interaction, $P = 0.075$; intercept, $P = 0.783$). In the ANCOVA for species-rich families within sites (Fig. 3), the homogeneity of slopes assumption was rejected for the Fabaceae for Panama ($P = 0.0054$) and Moraceae for Yasuni ($P = 0.0058$), but not for Fabaceae for Yasuni ($P = 0.179$).

WD_{rad} was significantly positively correlated with RGR and sapling mortality for Yasuni ($P = 0.013$ and 0.0013 , respectively), but when WD_{ctr} was included in the model ($RGR = WD_{ctr} \times WD_{rad}$), WD_{rad} was no longer significant. In models including WD_{ctr} , WD_{rad} and interactions (Table 1), WD_{ctr} was significantly correlated with sapling mortality, sapling RGR, maximum DBH and marginally significantly correlated with maximum height. Results from PICs were similar, although generally somewhat lower in significance. Neither WD_{rad} nor the $WD_{ctr} \times WD_{rad}$ interaction was significantly related to mortality, growth or size in species-level correlations. For PIC correlations, WD_{rad} was significant for sapling mortality in Panama, RGR in Yasuni and marginally significant for maximum height for Panama. $WD_{ctr} \times WD_{rad}$ interactions were marginally significantly correlated with RGR in Panama.

We found that 36% of mean WD variation was explained at the genus level, 22% at the family level and 19% at the order level, with 23% unexplained, that is,

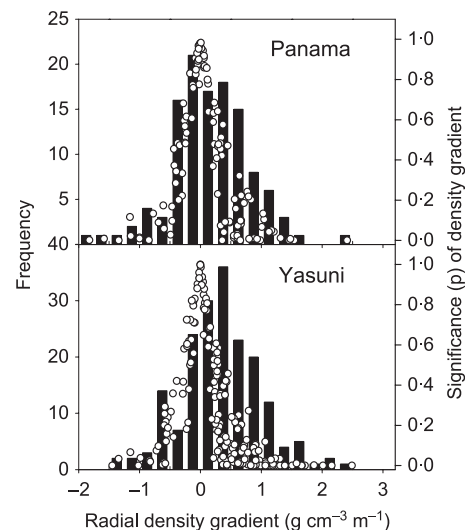


Fig. 2. Frequency (black bars) of radial wood density gradients of 118 tree species from Panama (top) and 186 from Yasuni, Ecuador (bottom) measured as the linear regression coefficient of density vs. distance along the radius. Positive gradient means density is increasing towards the bark. Circles indicate whether the density/distance correlation is significant (i.e. a radial density gradient $\neq 0$; P -value < 0.05 if) for each species.

variation at the species and individual (random) level (Fig. 4). The contribution of genus, family and order-level variation to WD_{rad} was 3%, 10% and 26%, respectively,

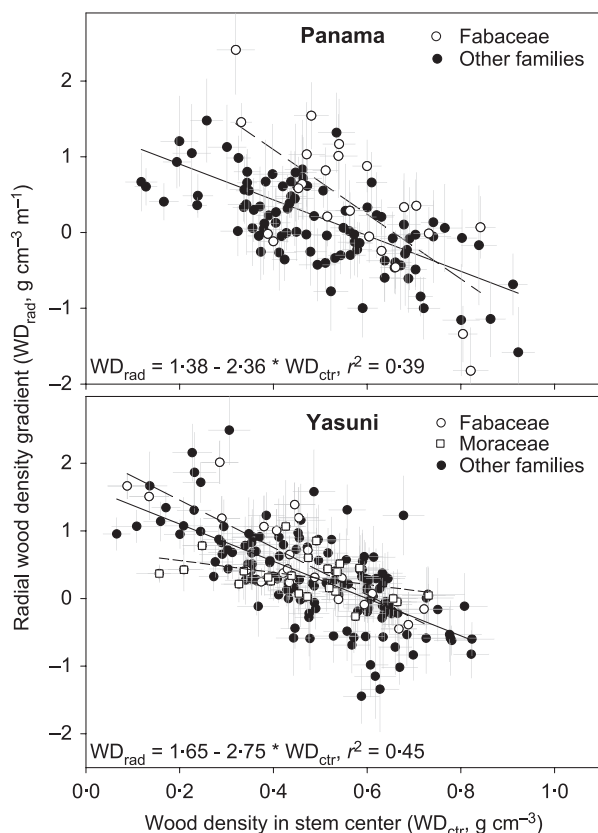


Fig. 3. Relationship between wood density in the stem centre and radial density gradients in 118 tree species from Panama and 186 from Yasuni. Both parameters were obtained as the linear regression coefficients of density vs. distance along the radius for the individual species. Families with >20 species are represented with empty symbols (\circ : Fabaceae and \square : Moraceae). The solid regression lines are for all species, the broken lines for Fabaceae (short dash) and Moraceae (long dash). Thin lines for each symbol indicate standard errors of the regression estimates.

with a much larger proportion of variation (61%) at the species level or unexplained (Fig. 4).

Discussion

Mean wood densities around BCI (0.570) and at Yasuni (0.597) were somewhat lower than in 5966 tropical species (0.61 ± 0.17 , Zanne *et al.* 2009) and other densities previously reported from wet Central American (0.602) and north-western Amazon (0.614) forests (Chave *et al.* 2006). Based on studies on WD across the neotropics (Baker *et al.* 2004; Malhi *et al.* 2006), the low mean WD at our two sites is consistent with their relatively fertile soils and rapid forest dynamics.

We found that in a substantial number of species from both forests, WD increased significantly towards the bark (Fig. 2), and in a number proportion of species, WD decreased. In addition to strong radial gradients in many trees, we found a surprisingly strong correlation ($r^2 = 0.39$ for Panama and 0.45 for Yasuni) between the density gradient and the inner density close to the centre. We consid-

ered that this correlation might be a result of the data structure with many regressions with rather few data points, but permutations with random sequences of samples (see Methods) showed that only a small part of the correlation can be explained by such a random effect. Because trees with medium initial density tended to show no radial gradient and those with high initial density a reduction in density towards the bark, outer wood density in larger trees converged somewhat, although not to the degree that outer wood tends to be of uniform density.

On average, in species with a juvenile WD <0.6, the wood tends to become denser towards the outer wood, and in trees with an initial density >0.6, the wood tends to become lighter (Fig. 3). This suggests that differences in the environment and life histories that drive WD are more varied for juvenile than for adult trees. This is plausible because whereas saplings can be found from large gaps to the dense understorey, where they are either fully exposed to sun and wind or completely sheltered, nearly all larger trees are growing among competitors with more similar environmental factors that may demand mechanic or hydraulic adjustments in wood structure.

We also found that WD_{ctr} was significantly correlated with demographic parameters along the pioneer-shade-tolerant gradient as well as tree size, confirming similar results for mean WD (Chao *et al.* 2008; Poorter *et al.* 2008; Chave *et al.* 2009; Kraft *et al.* 2010). The correlation of radial density gradients with demographic parameters was weaker, and when WD_{ctr} was included in the models, we found significant relationships only with phylogenetically independent contrasts for sapling mortality for Panama and for growth for Yasuni. This gives only partial support to the idea that radial density gradients are also related to the pioneer-shade-tolerant continuum, as this correlation appears to be mostly indirect because both are related to higher inner density. Generally, the correlations were not entirely but largely independent from the phylogenetic relationship between species as shown in the similar species-wise and PIC correlations.

EXPLANATIONS FOR DENSITY GRADIENTS

The most common explanation for a radial increase in WD, particularly in pioneers, is that young trees regenerating in high-light conditions face a high selective pressure to quickly grow in height or else they would be out-competed by faster growers (Woodcock & Shier 2002). Later, denser wood is produced to confer mechanical stability. Recently published models of tree mechanics disagree whether with a given investment in biomass a tree with high WD and smaller diameter will be more or less mechanically stable than a thicker tree with low WD (Anten & Schieving 2010; Larjavaara & Muller-Landau 2010; Niklas & Spatz 2010). While this discussion questions the general function of dense wood, a radial increase in density will always be a mechanical advantage compared to radial decreases because building a cylinder with

Table 1. Multiple regression testing the correlation between inner wood density (WD_{ctr}) and radial density gradients (WD_{rad}) and inner density \times density gradient interactions and maximum tree size (only available for Barro Colorado Island, Panama) and demographic parameters. RGR_{95} is the 95th percentile values of relative growth rates of saplings, M_{25} is the mortality rate for the 25% of saplings of each species with the smallest RGR in the previous census interval. Wood samples for density were collected from trees sampled within 15 km from BCI and within 2 km from the Yasuni plot, other parameters were obtained from long-term studies on BCI and at Yasuni

Independent variable	WD_{ctr} Estimate	P	WD_{rad} Estimate	P	$WD_{ctr} \times WD_{rad}$ Estimate	P	r^2	DF
Species								
BCI: Maximum height	-15.5	0.062	-275	0.559	-93.7	0.910	0.059	60
BCI: Maximum diameter	-6.93	0.019	-162	0.333	78.3	0.790	0.089	60
BCI: RGR_{95}	-1.16	<0.0001	-8.07	0.788	4.46	0.931	0.183	36
Yasuni: RGR_{95}	-2.60	<0.0001	-9.11	0.643	-18.23	0.649	0.411	73
BCI: M_{25}	-1.72	0.041	-54.23	0.281	21.56	0.803	0.127	36
Yasuni: M_{25}	-3.51	0.001	-0.52	0.991	17.34	0.861	0.329	52
PIC								
BCI Maximum height	-15.9	0.114	-392.7	0.062	3832	0.444	0.059	60
BCI Maximum diameter	-5.71	0.084	-81.3	0.235	-676	0.681	0.057	60
BCI: RGR_{95}	-1.85	0.001	-11.19	0.379	-943	0.070	0.299	36
Yasuni: RGR_{95}	-2.37	<0.0001	-21.79	0.015	-560	0.201	0.279	73
BCI: M_{25}	-1.84	0.019	-51.35	0.005	94.2	0.898	0.210	36
Yasuni: M_{25}	-2.97	0.002	9.69	0.584	1124	0.295	0.295	52

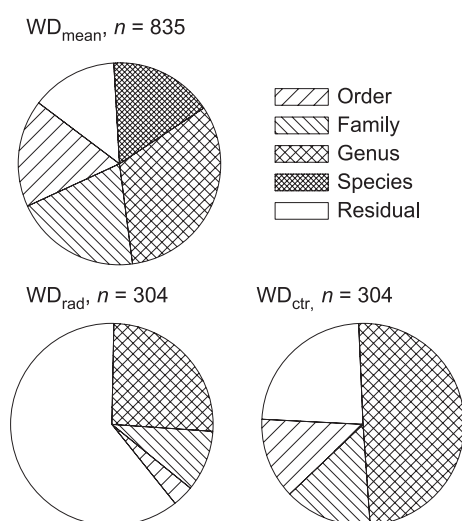


Fig. 4. Proportion of variance at the order, family, genus and species level to mean wood density (WD_{mean}), the radial wood density gradient (WD_{rad}) and density estimated for the centre in trees (WD_{ctr}) from tropical wet forests in Panama and Ecuador. The residual is the variance explained at the sample level for WD_{mean} and the species level for WD_{rad} and WD_{ctr} where species-wise regressions were used and the variance within species was not obtained.

the strongest material on the outside will guarantee the strongest cylinder, all else equal. If denser outer wood provides greater stability at a given size and biomass investment, can having higher density inside confer any mechanical advantage? Juveniles of shade-tolerant trees regenerating in the understorey have to survive for decades under low light with little prospect of fast growth. Here, investing in extra durable wood that resists falling branches and fungal attack may be an advantage given the trade-off between wood density and mortality (Poorter *et al.* 2008; Chave *et al.* 2009) and the particularly strong

increase in impact resistance with WD (USDA 1999). If these trees grow out of the darkest understorey to more favourable light conditions, such extra strong wood may no longer be needed and trees invest in faster diameter and height growth.

Alternatively a decline in wood density towards the bark, which is less common than an increase, may be the result of heartwood formation, that is, the deposition of extractives in the inner wood (Parolin 2002). Typically, a few per cent of heartwood, and generally less for sapwood, are extractives, but in some species including *Eucalyptus* and *Larix decidua*, this may amount to 30% of heartwood biomass (Hillis 1987; Grabner *et al.* 2005). In our trees, inner WD was never more than 22% higher than outer wood. Little is known about the amount of heartwood-forming extractives in most tropical trees (in teak heartwood extractives make up 5–8% of dry mass; Lukmandaru & Takahashi 2009), but if species with a negative density gradient have a high amount of extractives, this alone might explain the negative radial density gradients. In this case, the high inner wood density in these species would be unrelated to mechanical needs but reflect investment in protecting the wood against rot, the main function of extractives, which add little or nothing to mechanical strength. Analysing the proportion of extractives by comparing WD of extracted and raw wood of a number of trees with different density gradients could solve this question. In combination with demographic traits, this would also show the relative investment in avoiding death through either mechanical failure or pathogen attack.

A hydraulic explanation for radial variation in WD draws on the positive correlations between WD and embolism (and thus drought) resistance (Hacke *et al.* 2001; Pratt *et al.* 2007; Markensteijn *et al.* 2011). Wood density was found to be negatively correlated with hydraulic conductance in some tropical tree communities (Markesteijn *et al.*

2011) but not in others (Poorter *et al.* 2009; Russo *et al.* 2010), and a global survey found that WD accounts for only 2% of the variation in conductivity (Zanne *et al.* 2010). Juvenile wood is sometimes more resistant to cavitation than mature wood, which may be necessary as small trees have lower stem water storage capacitance and less developed root systems and are thus more frequently experiencing high water tension (Lachenbruch, Moore & Evans 2011). However, if drought resistance was the reason of high juvenile WD, we would expect that high juvenile (relative to adult) drought resistance should be much more important for species regenerating in sunny gaps than in trees in the shady and humid understorey. This should result in high juvenile density in light and low density in shade regenerating species, the opposite from what we find.

The ability to transport water efficiently under conditions of high potential growth and water demand, as well as the capacity to bridge times with low water supply drawing on internal storage, is likely more important for small trees in gaps than in the understorey. Thus, if there is a negative correlation between WD and hydraulic conductance in the species studied, we would expect these drivers to produce the radial density gradient found, in parallel or in addition to the mechanical and pathogen resistance functions outlined above.

Knowing which changes in wood structure result in changes in wood density may help to elucidate the adaptational significance of radial density gradients. Detailed anatomical measurements are laborious but have been carried out for the pioneer *Heliocarpus appendiculatu* (McDonald, Williamson & Wiemann 1995) where 85% of the variation in WD was explained by the change from a high proportion of axial parenchyma to fibres, whereas fibre wall thickness or lumen diameter explained only about 6%. As water is transported in tracheid lumina and fibres confer strength, changes in WD in this species are not or only to a minor extent driven by the need to adjust water transport capacity. We therefore believe that hydraulics play no or only a very minor role in driving radial WD gradients in tropical wet forest trees.

The correlation between WD and WD gradients did not differ between the two wet forests studied, suggesting it might hold for similar forests globally. In addition to studying the radial variation in wood anatomy in more detail, investigating whether the $WD_{ctr}:WD_{rad}$ correlation found differs from that in forests that are drier, more open or of smaller stature, would also help to elucidate whether drought resistance or the challenges to survive in the understorey play a role. Based on the discussion above, we expect that dry and more open forests have a very similar correlation but mostly lack trees with WD decreasing from stem centre to bark.

PHYLOGENETIC EFFECTS

Wood density carries a strong phylogenetic signal with 74% of species-level variation explained at the genus and

34% at the family level (Chave *et al.* 2006). This is similar to our data (the 74% of Chave *et al.* correspond to the sum of our genus-, family- and order-level variation, which is 77%), but the proportion of WD_{rad} we can explain at the genus or higher levels was only 39%. Are radial density gradients also conserved independent of the close relationship with mean or inner density? Generally, phylogenetically independent contrasts were similar to a correlation across species (Table 1), but the WD : WD_{rad} regression of Fabaceae and Moraceae differed from that of other families. Legume wood often features large, alate, paratracheal parenchyma, but whether this in any way affects wood mechanics and as a consequence, trees have to compensate by increasing wood density faster in legumes or slower in Moraceae is unknown. However, the different relationship between inner WD and the radial density gradient we found does suggest that in some tree families, the balance between the requirements for growth and strength during ontogeny differs from others. More detailed analysis of how different growth conditions affect WD, mechanistic models that include density gradients and understanding how other wood functional traits are related to WD would improve our understanding of the wood economics spectrum.

IMPORTANCE FOR BIOMASS ESTIMATES

Models for biomass and carbon estimates typically include a measure of tree size (dbh and perhaps height) and mean wood density (Chave *et al.* 2005), although not accounting for density gradients may result in substantial errors in biomass estimates (Nogueira, Fearnside & Nelson 2008; Nock *et al.* 2009). When WD of full stem discs is measured, this avoids having to account for possible radial gradients because a disc provides a weighted mean. Comparing WD between the full disc and heartwood shows that in species with high-density heartwood, the density of heartwood is close to or higher than in the full disc, whereas in species with light heartwood, heartwood density yields a substantial underestimate (Nogueira, Fearnside & Nelson 2008), which is what we would expect from the pattern of density gradients we found. Alternatively, where cutting trees to obtain full discs is not possible, it was suggested to take wood cores to the stem centre as a measure of mean WD (Chave *et al.* 2006). Moreover, using the mean density of a full disc or a core to the stem centre is an only partial solution. In a stem, the outer wood covers a greater area and contributes more to volume, which means that, in trees with density gradients, a core will yield a mean that over-represents values near the centre of the trunk. A stem disc does provide a correct weighted mean, but only for the size of the sampled tree. In the case of WD increasing towards the bark, the weighted mean WD of a sample stem of a given size represents an underestimate for a larger stem with more wood of high WD on the outside than the sample stem and an overestimate for a smaller stem. In other words, the

weighted mean that a stem disc provides is correct only for a stem of the size of the tree sampled, which is a correct mean for the population only if the size of the sampled tree represents the weighted mean (weighted in terms of the wood density estimate, not the population stem diameters) of the population.

Assuming that the density gradient is linear, knowing the radial WD gradient of a species (rather than inner and outer densities only) enables to calculate the correct mean density depending on tree size. Although we found that other functions to describe the density gradient overall were not superior to a linear model, this assumption will not always be correct and should be verified, perhaps by a finer-scale analysis of density variation. Given that the potential errors of either completely ignoring density gradients or extrapolating a density gradient are not trivial, we propose to measure wood density gradients and to include the larger trees of each species when sampling wood density for biomass estimates. Breaking down a core into several segments does not add much extra work, but, apart from providing insight into the ontogenetic adjustments during a tree's life, can contribute to improving biomass estimates. As long as such data are not available for most species, the correlation between inner density and the density gradient among a large number of species could be used to estimate species-specific density gradients from inner density alone. The high coefficient of determination and the similarity of this regression for two rain forests (Fig. 3) suggest this approach may produce better estimates than ignoring density gradients completely.

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