

Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community

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Summary

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- Wood density plays a central role in the life-history variation of trees, and has important consequences for mechanical properties of wood, stem and branches, and tree architecture.
- Wood density, modulus of rupture, modulus of elasticity, and safety factors for buckling and bending were determined for saplings of 30 Bolivian rain forest tree species, and related to two important life-history axes: juvenile light demand and maximum adult stature.
- Wood density was strongly positively related to wood strength and stiffness. Species safety factor for buckling was positively related to wood density and stiffness, but tree architecture (height : diameter ratio) was the strongest determinant of mechanical safety. Shade-tolerant species had dense and tough wood to enhance survival in the understorey, whereas pioneer species had low-density wood and low safety margins to enhance growth in gaps. Pioneer and shade-tolerant species showed opposite relationships between species traits and adult stature.
- Light demand and adult stature affect wood properties, tree architecture and plant performance in different ways, contributing to the coexistence of rain forest species.

Key words: Bolivia, maximum height, modulus of elasticity, modulus of rupture, safety factor, shade tolerance, tropical rain forest, wood density.

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Introduction

Life-history theory predicts that species specialized for ephemeral high-resource environments should pre-empt resources by having fast growth, small reproductive size and rapid completion of their life cycle (MacArthur & Wilson, 1967). By contrast, species specialized for stable, low-resource environments should have high survival rates, large reproductive size and a long life span. Wood density plays a central role in the life-history variation of tree species as low-density wood is cheap to construct, allowing for rapid growth in stem dimensions, whereas high-density wood results in a persistent structure, allowing for a high survival rate and long life span. Variation in wood density has important consequences for the mechanical properties of wood, and hence for the mechanical safety of stems and branches (Niklas, 1993; Sterck & Bongers, 1998), which, in turn, determine the

architecture (Sterck *et al.*, 2001; Poorter *et al.*, 2003, 2006), growth (King *et al.*, 2005) and survival (Alvarez, 2005) of trees.

The density of the solid component of wood is surprisingly similar among species, approx. 1.5 g cm⁻³ (Williamson, 1984). Interspecific variation in wood density is therefore caused mainly by variations in the amount of intra- and extracellular spaces (Turner, 2001). Within tree communities, species show a large variation in wood density, typically varying from 0.2 to 1.0 g cm⁻³ (ter Steege & Hammond, 2001; Muller-Landau, 2004), and with maxima up to 1.3. Wood density is, in general, strongly and positively correlated with the stiffness, bending strength and compression strength of wood. Stiffness is the amount of deflection of a wood member under a known force, commonly referred to as the modulus of elasticity (MOE). Bending strength is the maximum amount of bending stress that can be applied on a cross-section of wood without rupture

or mechanical failure, also known as the modulus of rupture (MOR). Compression strength (CS) is the maximum amount of stress that can be applied in compression without rupture or failure (Gere, 2004). A higher MOE, MOR and CS indicate that a tree is better able to maintain its structural integrity without risk of mechanical failure, but comes at the expense of reduced growth because of the high construction costs of the wood. Mechanical properties are typically determined for oven-dry wood (Tsoumis, 1991). However, to understand the mechanical stability of living trees it is much more meaningful to determine the mechanical properties of water-saturated wood, as dry wood is much stronger than water-saturated wood (Kollmann & Côté, 1968).

Mechanical properties put constraints on the shape and dimensions of stems and branches. The critical buckling height indicates the maximum height a vertical stem can attain before it buckles under its own weight (Mosbrugger, 1990), and is determined by the wood density, MOE and diameter of the tree (McMahon, 1973). The buckling safety factor is the ratio of buckling height to observed height, and indicates the safety margins that trees maintain against dynamic loads such as wind, rain and falling debris. Stems and branches have to resist bending stresses. In stems, bending moments originate mainly from an inclined stem, wind loads and/or asymmetrical weight distribution of the crown; in lateral branches, bending moments originate mainly from their own weight, horizontal length and wind. The critical bending diameter is the diameter under which a stem or branch suspended on one side would break under the loads experienced (Mattheck, 1998). The critical bending diameter depends on the weight, diameter and arm of the stem or branch, and the MOR (Gere, 2004). The bending safety factor is the ratio between observed diameter and critical bending diameter.

Safety factors for buckling and bending are important determinants of the risk of mechanical failure (Putz *et al.*, 1983), tree architecture (Sterck *et al.*, 2001; Poorter *et al.*, 2003), and the efficiency and rate at which trees grow towards the canopy (Poorter *et al.*, 2003; King *et al.*, 2005). Ultimately, they may determine the environmental conditions under which tree species may be successful. In tropical rain forests, light is thought to be the most limiting factor for plant growth and survival, and light availability increases horizontally from the understorey to gap centres, and vertically from the forest floor to the canopy. Shade-tolerant and pioneer species partition the horizontal light gradient, and small understorey and large canopy species partition the vertical height gradient. Juvenile light demand and maximum adult stature therefore capture the major variation in life-history traits found among tree species (Turner, 2001; Poorter *et al.*, 2006). Shade-tolerant species are thought to grow at large safety margins to resist dynamic loads by falling debris and increase survival in the understorey (King, 1986), whereas pioneer species are thought to grow at small safety margins to maximize height gain and compete effectively with neighbouring trees for light and space in gaps. Small understorey species survive stem breakage better than

tall canopy species (Ickes *et al.*, 2003), suggesting that they are adapted to higher disturbance regime. It can also be hypothesized that small understorey species that are regularly hit by falling debris have larger safety margins than large canopy trees, which have to grow efficiently in height to rapidly attain their large reproductive size. Hard data are scarce for these hypotheses.

Ideally, a community approach should be taken to obtain insight into the importance of wood density and mechanical properties for life-history variation in trees. To date, such large-scale, comparative data sets are lacking, and most of our information comes from data compilations for mature trees from a wide range of ecosystems, measured using different methodologies (Clarke, 1937; Niklas, 1992). In this study, we evaluate the wood density and mechanical properties of saplings of 30 coexisting rain forest tree species, and relate them to quantitative measures of light demand and maximum adult height. We evaluate: how the MOE, MOR and CS are related to the wood density of the species, and how safety factors for bending and buckling are determined by their underlying components. We predict that the wood density, stiffness, strength and safety factors for buckling and bending decrease with the light requirements and maximum adult height of the species.

Materials and Methods

Study site

Research was conducted within the 100 000-ha forestry concession La Chonta (15°47' S, 62°55' W), located in the department of Santa Cruz, Bolivia. The forest can be classified as a lowland tropical moist forest. Mean annual temperature is 25.3°C and mean annual precipitation is 1520 mm with a dry season (<100 mm rain per month) lasting from May until October. The forest cover is seasonal with about one-third of the canopy species losing their leaves during the dry season. The forest has an average canopy height of 25 m; stem density of 367 ha⁻¹; basal area of 19.3 m² ha⁻¹; and species richness of 59 ha⁻¹ [all data for trees ≥ 10 cm diameter at breast height (dbh), Instituto Boliviano de Investigación Forestal (IBIF), unpublished data]. The area is part of a large-scale, long-term silvicultural research project of the IBIF.

Species selection

Thirty species of tree belonging to 21 families were selected for this study (Table 1). The species belonged to the most abundant species in the community, and differed in adult stature and shade tolerance. The maximum adult stature or potential height (H_{\max}) was obtained from Poorter *et al.* (2006). Species were classified into 20 shade-tolerant species that can establish and survive in the shade, and 10 pioneers that need high light conditions for successful regeneration (Poorter *et al.*, 2006). Light demand varies continuously among

Table 1 Overview of the 30 study species, their shade-tolerance guild (ST, shade-tolerant; P, pioneer); juvenile crown exposure (CE_{juv}); maximum adult stature (H_{max}); saturated and dry wood density (ρ) of vertical stems and horizontal branches; modulus of rupture (MOR); compression strength (CS); modulus of elasticity (MOE); and safety factors (SF) for buckling and bending

Species	Family	Guild	CE_{juv}	H_{max} (m)	ρ_{sat} branch (g cm ⁻³)	ρ_{dry} branch (g cm ⁻³)	ρ_{sat} stem (g cm ⁻³)	ρ_{dry} stem (g cm ⁻³)	MOR (N mm ⁻²)	CS (N mm ⁻²)	MOE (N mm ⁻²)	SF buckling (m m ⁻¹)	SF bending branch (mm mm ⁻¹)	SF bending stem (mm mm ⁻¹)
<i>Alibertia verrucosa</i> S. Moore	Rubiaceae	ST	1.35	13	0.99	0.53	1.22	0.56	76.8	28.4	6682	3.20	2.15	4.82
<i>Ampelocera ruizii</i> Klotzsch	Ulmaceae	ST	1.35	36	1.05	0.48	1.13	0.53	64.0	24.3	6252	2.62	2.22	2.45
<i>Aspidosperma cylindrocarpon</i> Müll. Arg.	Apocynaceae	ST	1.75	28	1.09	0.47	1.08	0.43	60.1	26.3	4242	2.30	1.88	2.58
<i>Aspidosperma rigidum</i> Rusby	Apocynaceae	ST	1.56	30	1.16	0.51	1.09	0.46	59.8	23.5	4875	2.17	1.88	3.70
<i>Casearia</i> sp.	Flacourtiaceae	ST	1.39	6	1.14	0.52	1.16	0.56	66.2	21.1	5383	2.78	2.26	2.98
<i>Cecropia concolor</i> Willd.	Cecropiaceae	P	2.44	33	–	–	0.75	0.15	25.2	10.3	4705	2.54	–	2.75
<i>Centrolobium microchaete</i> (C. Martius ex Benth.) Lima ex G.P. Lewis	Fabaceae	P	1.94	26	0.87	0.34	0.90	0.33	42.5	16.0	5694	2.68	1.84	2.63
<i>Cupania cinerea</i> Poepp. & Endl.	Sapindaceae	ST	1.79	22	1.08	0.50	1.11	0.50	64.4	24.1	7578	2.33	2.22	2.63
<i>Erythrochiton fallax</i> Kallunki	Rutaceae	ST	1.27	5	1.07	0.42	1.11	0.45	45.6	17.8	2302	2.53	2.25	3.96
<i>Eugenia florida</i> DC.	Myrtaceae	ST	1.52	8	1.15	0.56	1.27	0.54	68.0	23.8	7454	2.90	1.81	3.10
<i>Gallesia integrifolia</i> (Sprengel) Harms	Phytolaccaceae	P	1.84	42	1.02	0.39	0.99	0.35	48.9	18.0	5789	2.86	1.79	3.31
<i>Guarea guidonia</i> (L.) Sleumer	Meliaceae	ST	1.33	9	1.11	0.36	1.06	0.41	50.9	19.8	5119	2.62	2.43	3.36
<i>Heliocarpus americanus</i> L.	Tiliaceae	P	2.36	22	0.83	0.18	0.79	0.20	13.8	5.4	2386	2.24	1.45	2.04
<i>Hirtella triandra</i> Sw.	Chrysobalanaceae	ST	1.28	11	1.15	0.58	1.12	0.54	80.3	24.8	7248	2.80	2.05	3.60
<i>Hura crepitans</i> L.	Euphorbiaceae	ST	1.62	44	0.84	0.24	0.85	0.25	26.9	11.6	3588	2.74	1.70	2.14
<i>Jacaratia spinosa</i> (Aubl.) A. DC.	Caricaceae	P	2.02	21	0.93	0.12	0.98	0.11	7.6	3.5	898	1.55	1.62	2.19
<i>Licaria triandra</i> (Sw.) Kosterm.	Lauraceae	ST	1.35	14	1.04	0.49	1.06	0.47	61.4	21.7	5938	3.31	1.90	3.78
<i>Myrciaria</i> sp.	Myrtaceae	ST	1.45	25	1.12	0.58	1.16	0.53	79.1	29.9	6318	2.79	2.19	3.69
<i>Ocotea guianensis</i> (Aubl.)	Lauraceae	P	1.54	25	0.91	0.42	0.86	0.40	56.3	20.8	6322	2.59	1.84	2.93
<i>Ocotea</i> sp.1	Lauraceae	ST	1.37	27	0.97	0.34	1.05	0.32	51.7	18.3	5179	3.22	2.30	4.71
<i>Peschiera australis</i> (Muell. Arg.) Miers	Apocynaceae	ST	1.38	16	1.05	0.37	1.06	0.34	44.9	18.2	3475	2.76	1.92	2.77
<i>Pouteria macrophylla</i> (Lam.) Eyma	Sapotaceae	ST	1.55	29	1.09	0.43	1.11	0.41	43.4	17.0	4171	2.30	1.91	2.82
<i>Pouteria nemorosa</i> Baehni	Sapotaceae	ST	1.57	35	1.10	0.46	1.12	0.44	53.6	18.4	5265	2.16	2.02	2.92
<i>Pseudolmedia laevis</i> (Ruiz & Pavón) J.F. Macbr.	Moraceae	ST	1.32	35	1.04	0.48	1.19	0.45	50.7	18.2	4039	2.59	2.19	5.00
<i>Sapium glandulosum</i> (L.) Morong	Euphorbiaceae	P	2.23	31	0.87	0.29	0.95	0.27	35.1	15.2	4494	2.70	1.74	2.59
<i>Stylogyne ambigua</i> (Mart.) Mez	Myrsinaceae	ST	1.46	10	1.09	0.42	1.22	0.43	56.8	20.3	5291	3.06	2.11	4.50
<i>Sweetia fruticosa</i> Spreng.	Fabaceae	P	1.91	34	1.14	0.56	1.13	0.54	87.6	29.2	7765	2.71	2.01	2.46
<i>Terminalia oblonga</i> (Ruiz & Pavón) Steudel	Combretaceae	ST	1.88	34	0.96	0.40	1.00	0.37	42.2	15.5	3996	2.81	2.11	3.18
<i>Trema micrantha</i> (L.) Blume	Ulmaceae	P	2.52	31	0.75	0.23	0.74	0.20	25.1	11.4	3533	2.30	1.58	2.68
<i>Urera caracasana</i> (Jacq.) Gaudich ex Griseb.	Urticaceae	P	1.99	13	0.94	0.16	0.93	0.18	16.2	3.4	2614	2.23	1.39	1.75

species. In a separate study (Poorter *et al.*, 2006), we estimated the height and crown exposure (cf. Dawkins & Field, 1978) for 662 (range 41–9319) individuals per species. Crown exposure (CE) is measured as: 1 if a tree does not receive any direct light; 2 if it receives lateral light; 3 if it receives overhead light on part of the crown; 4 when it receives full overhead light on the whole crown; 5 when it has an emergent crown that receives light from all directions. The CE can be measured repeatably (the average difference between two independent observers is 0.1 ± 0.01 SE), and there is a good relation between CE and canopy openness (Davies *et al.*, 1998). For each species we related CE to tree height using a multinomial regression analysis (Poorter *et al.*, 2006, cf. Poorter *et al.*, 2005). Using the regression equation, the average juvenile CE at a standardized height of 2 m (CE_{juv}) was calculated.

Measurements

Five individuals per species were selected in the shade ($CE < 2.5$) and five individuals were selected in high light ($CE \geq 2.5$). The high- and low-light individuals did not differ significantly in their wood properties, and were therefore pooled for further analysis. The CE was estimated by two independent observers according to the adjusted Dawkins' crown exposure scale (Clark & Clark, 1992). The CE of the selected individuals did not differ between species (Kruskal–Wallis test, $\chi^2 = 8.96$, $P = 1.000$, $df = 29$) and on average was 2.3 (range 1–4). The average height was 2.9 m (range 1.8–4.0), dbh 17.8 mm (range 5.9–36.5).

For each sapling we determined the height, length of largest branch, dbh, stem diameter at 1 m from the growth tip, and branch diameter at the base of a large vital branch. For the terminal metre of the stem and the lowest branch, the angle with the horizontal, weight (including leaves) and position of the centre of gravity of the branch were measured. The centre of gravity, or mass centre, is the point where the resultant of the gravitational forces pulls on the branch. First the branch was separated from the tree. The centre of gravity was then determined by balancing the branch on a pencil. The point where the branch remained in a stable horizontal position was regarded as the working line of the centre of gravity.

Wood properties were determined using six samples from each individual: two from the lowest branch, two from the base, and two from the terminal metre of the stem. The green volume was calculated using length and diameters at the beginning and end of the sample, and the formula for volumes of cones. Green weight was measured on the day of collection. The saturated weight was determined after submerging a subset of the samples under water for 4–5 d. The dry weight was determined for another subset of samples after drying in an oven at 70°C. All densities were calculated by dividing weight (dry, green or saturated) by green volume. Wood density, strength and stiffness were measured on stem and branch samples that included the bark.

The bending strength (or MOR), CS and stiffness (or Young's MOE) were measured on 20-mm-thick samples taken from the stem base. Samples were water-saturated before measurement. As saturated wood is weaker than dry wood (Kollmann & Côté, 1968), these measurements indicate the minimum wood strength that is displayed by living trees in the forest. Samples had a length : height ratio ≥ 18 and a span : height ratio ≥ 15 , to minimize disturbing effects on the measurement of MOR (Kollmann & Côté, 1968). The MOR was determined using loading equipment (Tinius Olsen, Horsham, PA, USA), applying loads (± 1.25 kg) with a known speed until the maximum load was reached and the sample broke (mean test time 3 min; deflection speed varying between 1.5 and 3 mm s⁻¹). The formula for the MOR (N mm⁻²) for a sample with a circular cross-section and supported on two sides is:

$$MOR = (M_{max} \times z) / I = (1/4 F_{max} \times L \times R) / (1/4 \pi R^4) \quad \text{Eqn 1}$$

where M_{max} is the maximum bending moment (N mm); I is the second-order moment of area (mm⁴); z is the section modulus or distance between the centre of a cross-section and the outermost fibre (mm); F_{max} is the maximum load (N); L is the span (mm); and R is the radius (mm). In a circular cross-section $z = R$ and $I = 1/4 \pi R^4$ (Verruijt, 1993; Gere, 2004). The load and accompanied deflection were recorded for each load interval of 2.5 kg. MOE (N mm⁻²) was calculated based on the first linear, elastic part of the relationship between the load (F , N) and deflection (δ , mm):

$$\delta = (F \times L^3) / (48 \times MOE \times I) \quad \text{Eqn 2}$$

To determine the CS (N mm⁻²), 5-cm-high samples were prepared. The same loading equipment was used, but now the load was applied axially on the specimen until the maximum axial load P (N) was reached for a cross-section with area A (mm²), with a mean test time of 1 min:

$$CS = P/A \quad \text{Eqn 3}$$

Mechanical models

According to the Euler–Greenhill buckling formula (McMahon, 1973), the critical buckling height (H_{crit} , cm) is:

$$H_{crit} = 0.792(MOE/\rho_{sat})^{1/3} DBH^{2/3} \quad \text{Eqn 4}$$

where MOE is the modulus of elasticity (N cm⁻²); ρ_{sat} is the saturated wood density (g cm⁻³, but note that the gravitational force here is given per unit wood volume, in N cm⁻³); and dbh is diameter at breast height (cm). The formula assumes the shape of an untapered cylinder with its weight evenly distributed along the column height. It also assumes that the weight of leaves and branches equals the additional weight of the stem, by considering it a cylinder rather than a tapered stem (Holbrook & Putz, 1989). The buckling safety factor is the ratio of critical buckling height to observed height (H_{crit}/H_{obs}). The observed

height was calculated using the formula: $H_{\text{obs}} = H_{\text{tree}} - 130$ cm. This is the tree height above breast height, as the dbh was also taken at breast height.

Predicted minimum diameters (D_{min} , mm) of stems and branches were calculated for one-sided, supported cantilevers using the bending model. D_{min} was derived from the formula for applied bending stress, σ , on a circular cross-section with a known self-load (P , N) and horizontal arm length L_{cm} (mm) to the centre of mass:

$$\sigma = (M \times z) / I = (P \times L_{\text{cm}} \times R) / (1/4 \pi R^4) \leq \text{MOR} \quad \text{Eqn 5}$$

where $D_{\text{min}} = 2R$. The bending safety factor is the ratio of observed to predicted minimum diameter ($D_{\text{obs}} / D_{\text{min}}$).

Data analysis

First we explored the relationship between the mechanical wood properties of the 30 species, using linear regressions with MOR, CS and MOE as dependent factors, and dry, green and saturated wood density as independent factors. Differences between species were tested with a Kruskal–Wallis test, and differences between pioneers and shade-tolerant species were tested with a t -test. Second, we evaluated the consequences of wood properties on the mechanical stability of species, using buckling and bending cantilever theory. To identify how safety factors depend on wood properties, multiple linear regression analyses were used, in which all independent variables were entered at the same time. Third, we related the variation in wood properties and mechanical safety to the life-history variation among species (juvenile CE and adult stature) using regression analyses. Relationships between functional traits and adult stature might be different for pioneer and shade-tolerant species (Falster & Westoby, 2005). We therefore carried out an ANCOVA analysis with adult stature as a covariate, shade-tolerance group as a factor, and the interaction between adult stature and shade tolerance group. As we used adult stature as a predictor for the functional traits, we used normal model I regression. Regressions with adult stature were shown separately for pioneer and shade-tolerant species. *Jacaratia spinosa* was an outlier (it has wood with low dry density, high water content and extremely stout stems), and results are therefore reported with and without *Jacaratia*.

Results

Mechanical properties of wood

Wood strength and stiffness were strongly related to wood density, the MOR, CS and MOE increased with density (Fig. 1). Dry wood density was the strongest predictor of wood strength and stiffness, followed by saturated and green density. The relationship between mechanical properties and wood density was strongest for MOR, followed by CS and MOE. *Jacaratia*

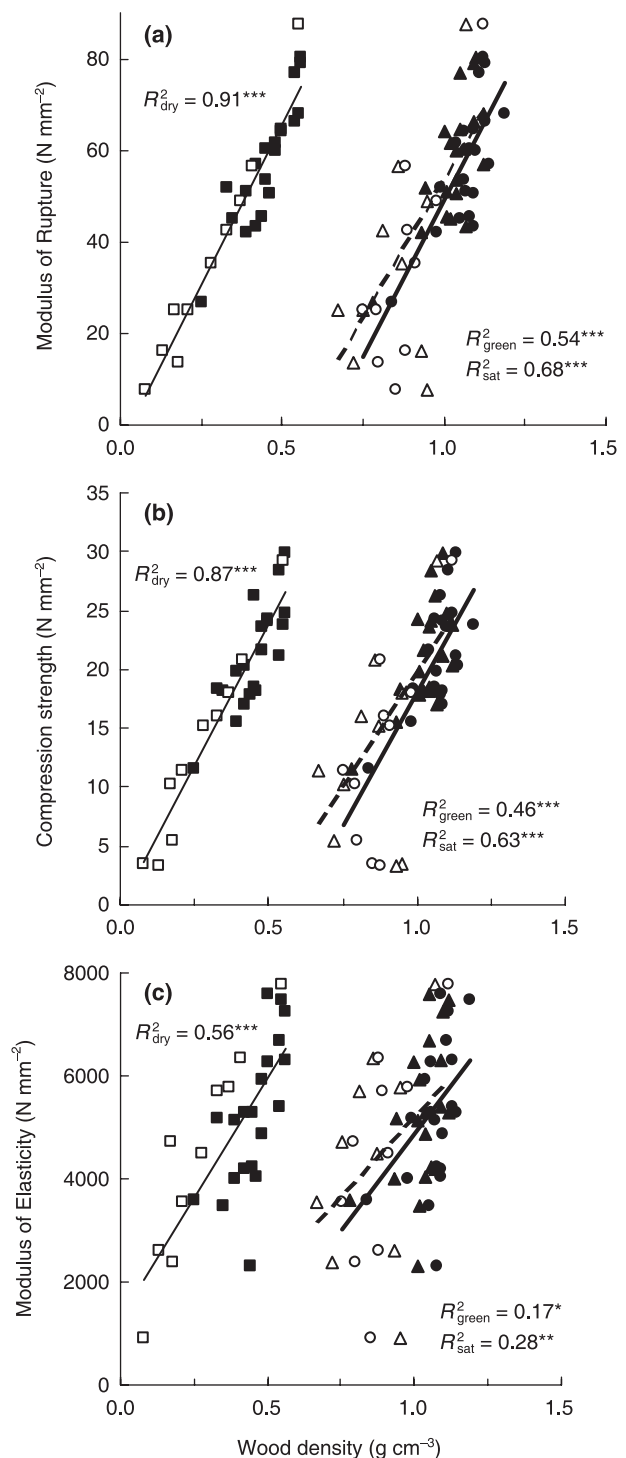


Fig. 1 Relationship between (a) modulus of rupture; (b) compression strength; (c) modulus of elasticity and dry (squares), green (triangles) and saturated (circles) wood density of 30 rain forest tree species. Closed symbols, shade-tolerant species; open symbols, pioneer species. Regression lines, coefficients of determination (R^2) and significance levels (*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$) are shown.

spinosa and *Urera caracasana* were outliers (Fig. 1). These species showed a moderate green and saturated density with a very low value of MOR, CS and MOE. There was also a positive relationship between MOR and MOE ($\text{MOE} = 1397 + 70.88 \times \text{MOR}$, $R^2 = 0.72$, $P < 0.001$, $n = 30$). Thus species with stronger wood tended to have stiffer wood.

Species differed significantly in their wood density, MOR and CS (Kruskal–Wallis test, $\chi^2 > 139$, $P < 0.001$, $df = 29$ in all cases). Pioneer and shade-tolerant species showed similar, positive relations between density and strength and stiffness. Pioneers had a significantly lower wood density, MOR and CS than shade-tolerants, but a similar MOE (Table 2).

Buckling and bending safety

Buckling safety varied from 1.6 to 3.3, and differed significantly among the 30 species (Kruskal–Wallis test, $\chi^2 = 87.2$, $P < 0.001$,

$df = 29$). Surprisingly, shade-tolerant and pioneer species had a similar buckling safety factor (Table 2). With a multiple regression, the safety factor for buckling was related to its underlying components. Species safety for buckling was positively related to MOE and dbh, and negatively to height and ρ_{sat} (Table 3). Height was the strongest determinant of interspecific variation in buckling safety, as indicated by the standardized regression coefficient, followed by MOE. The same results were found if *Jacaratia* was excluded from the analysis. Note that the bivariate correlation between safety for buckling and ρ_{sat} is positive rather than negative (Fig. 2a). This is because ρ_{sat} is strongly positively correlated with MOE (Fig. 1), and MOE has a strong positive effect on the buckling factor, overruling the negative direct effect of ρ_{sat} .

Vertical stems had a higher bending safety factor than horizontal branches (Fig. 3; paired samples *t*-test, $df = 28$, $t = -8.94$, $P < 0.001$). The vertical and horizontal bending safety

Variable	Shade-tolerant	Pioneer	<i>t</i>	<i>P</i>
Green density, horizontal (g cm^{-3})	1.09 (0.08)	0.86 (0.12)	3.93	***
Green density, vertical (g cm^{-3})	1.05 (0.09)	0.89 (0.13)	4.72	***
Saturated density, horizontal (g cm^{-3})	1.06 (0.08)	0.91 (0.11)	4.18	***
Saturated density, vertical (g cm^{-3})	1.11 (0.09)	0.90 (0.12)	5.18	***
Dry density, horizontal (g cm^{-3})	0.46 (0.09)	0.30 (0.14)	3.73	***
Dry density, vertical (g cm^{-3})	0.45 (0.08)	0.27 (0.13)	4.50	***
Compression strength (N mm^{-2})	21.1 (4.5)	13.3 (8.3)	2.80	*
Modulus of rupture (N mm^{-2})	57.3 (13.5)	35.8 (24.1)	3.15	**
Modulus of elasticity (N mm^{-2})	5220 (1431)	4420 (1082)	1.24	ns
Buckling safety factor (cm cm^{-1})	2.70 (0.34)	2.44 (0.38)	1.90	ns
Bending safety factor, horizontal (mm mm^{-1})	1.84 (0.19)	2.00 (0.20)	-0.90	ns
Bending safety factor, vertical (mm mm^{-1})	3.22 (0.83)	2.95 (0.45)	0.83	ns
Juvenile crown exposure (-)	1.69 (0.22)	2.46 (0.59)	-3.97	**
Maximum adult stature (m)	21.0 (11.1)	24.9 (5.9)	-1.28	ns

Mean values (\pm SE), results of a *t*-test (*t*) and significance levels (*P*) are shown. Significance levels are qualitatively similar if *Jacaratia spinosa* is excluded from the analysis. ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Table 2 Mechanical and architectural properties of shade-tolerant ($n = 20$) and pioneer ($n = 10$) rain forest tree species

Safety factor	Variable	With <i>Jacaratia</i>			Without <i>Jacaratia</i>		
		β	<i>P</i>	R^2	β	<i>P</i>	R^2
Buckling	ρ_{sat}	-0.42	***	0.90	-0.40	***	0.94
	MOE	0.90	***				
	dbh	0.48	***				
	Height	-1.09	***				
Horizontal bending	ρ_{sat}	0.26	ns	0.46	0.26	ns	0.43
	MOR	0.47	*		0.49		
	Branch diameter	0.07	ns		0.11	ns	
Vertical bending	ρ_{sat}	0.41	ns	0.35	0.58	*	0.40
	MOR	0.36	ns		0.21	ns	
	Stem diameter	0.28	ns		0.40	*	

Standardized regression coefficients (β), significance levels (*P*) and coefficients of determination (R^2) are shown. Analyses are presented with and without *Jacaratia spinosa*. ns, $P > 0.05$; †, $P = 0.06$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Table 3 Multiple linear regression of buckling and bending safety factor of 30 rain forest tree species on their underlying components. (buckling: saturated wood density (ρ_{sat}); modulus of elasticity (MOE); diameter at breast height (dbh); observed height; bending: saturated wood density (ρ_{sat}); modulus of rupture (MOR); diameter)

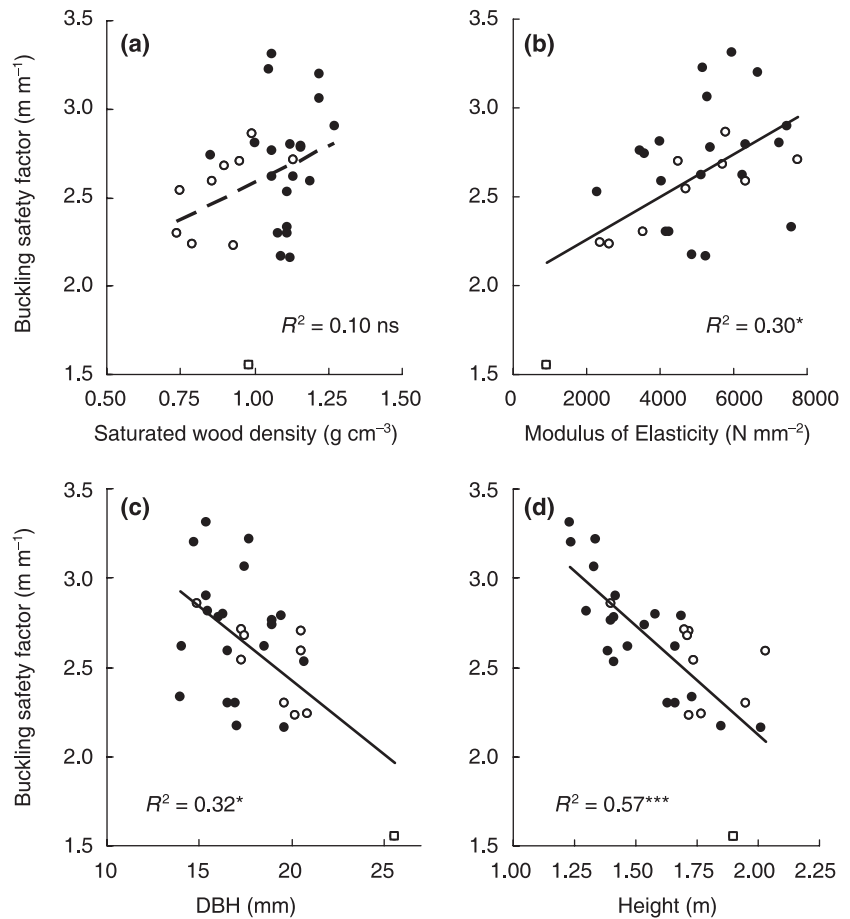


Fig. 2 Relationship between buckling safety factor and (a) saturated density (ρ_{sat}); (b) modulus of elasticity (MOE); (c) diameter at breast height (dbh); and (d) actual height of 30 rain forest tree species. Closed symbols, shade-tolerant species; open symbols, pioneer species. Regression lines, coefficients of determination (R^2) and significance levels (ns, $P > 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$) are shown. If the outlier *Jacaratia spinosa* (open square) is excluded from the regression analysis, the relationship with MOE becomes weaker ($R^2 = 0.16$, *) and the relationship with dbh disappears ($R^2 = 0.13$, ns). The relationship with the other two variables remains similar.

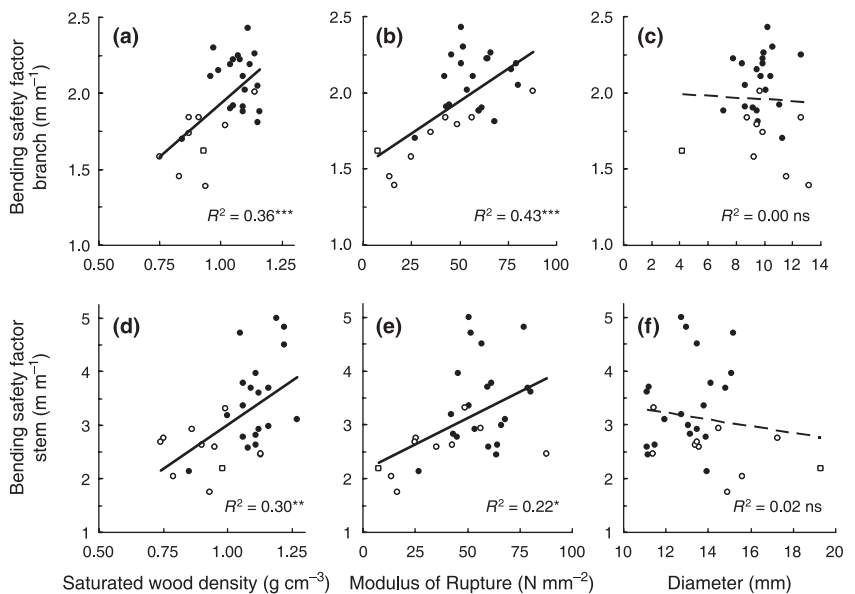


Fig. 3 Bending safety factor vs (a,d) saturated density; (b,e) modulus of rupture; (c,f) actual diameter. Bending safety factors are given for horizontal branches (a–c) and vertical stems (d–f) of 30 rain forest tree species. Closed symbols, shade-tolerant species; open symbols, pioneer species. Regression lines, coefficient of determination (R^2) and significance levels (ns, $P > 0.05$; *, $P \leq 0.05$; ***, $P \leq 0.001$) are shown. Relationships and significance levels are similar if *Jacaratia spinosa* (open square) is excluded from the regression analysis.

factors were positively correlated with each other (Pearson's $r = 0.63$, $n = 29$, $P < 0.001$). The safety factor for bending of vertical stems varied from 1.8 to 5.0, and differed among species ($\chi^2 = 122.6$, $P < 0.001$, $df = 29$). The bending safety factor for horizontal

branches varied from 1.4 to 2.4, and differed significantly among species (Kruskal–Wallis test, $\chi^2 = 106.5$, $P < 0.001$, $df = 28$). Shade-tolerant species, as a group, had a safety factor similar to pioneers for bending of horizontal branches and vertical stems (Table 2).

Bending safety of horizontal branches and stems correlated positively with ρ_{sat} and MOR, but was unaffected by the observed diameter (Fig. 3). The multiple regression analysis suggested that the interspecific differences in bending safety of horizontal branches were caused by variation in MOR, not in ρ_{sat} (Table 3). The multiple regression analysis did not show any significant direct effects of individual factors on the bending safety of stems. Note that the inclusion of *Jacaratia* resulted in significant effects of both stem diameter and ρ_{sat} on the bending safety of stems.

Life-history variation: average juvenile crown exposure and maximum adult stature

Maximum adult stature and CE_{juv} were positively correlated (Pearson's $r = 0.38$, $P = 0.04$, $n = 30$). For all species pooled, wood properties and safety factors correlated significantly with CE_{juv} , but not with maximum adult stature (Fig. 4).

Wood density and MOR correlated negatively with CE_{juv} , suggesting that species with light and weak wood occupy more open environments. The MOE was not related to CE_{juv} . Buckling and bending safety correlated negatively with CE, suggesting that species adapted to more open environments have lower mechanical safety margins.

Wood properties and mechanical safety were not correlated with maximum adult stature for all species pooled. ANCOVA analysis indicated that shade-tolerant and pioneer species had different relationships between biomechanical properties and adult stature (ANCOVA, shade tolerance group–maximum adult stature interaction, $F > 4.5$, $P < 0.044$ in all cases). When the shade-tolerant and pioneer groups were analysed separately, contrasting correlations of maximum adult stature with wood traits and safety were found for the two groups. When maximum adult stature increased, wood density, strength, stiffness and safety factors decreased for the shade group, but increased for the pioneer group (Fig. 4).

Discussion

Tree species show large variation in wood properties such as density and strength (Kollmann & Côté, 1968; Tsoumis, 1991; Reyes *et al.*, 1992; Niklas, 1993). In this study we explored wood property differences related to differences in mechanical safety and life-history traits for 30 species of a Bolivian tree community. We analysed how wood density was related to wood strength and elasticity, how wood density and strength influenced mechanical safety, and how wood properties and mechanical safety were associated with average CE and maximum adult stature.

Mechanical properties of wood

Mechanical properties (MOE, MOR and CS) increased with the density of the wood (Fig. 1; cf. Clarke, 1937; Kollmann & Côté, 1968; Chu, 1975; Tsoumis, 1991; Niklas, 1993).

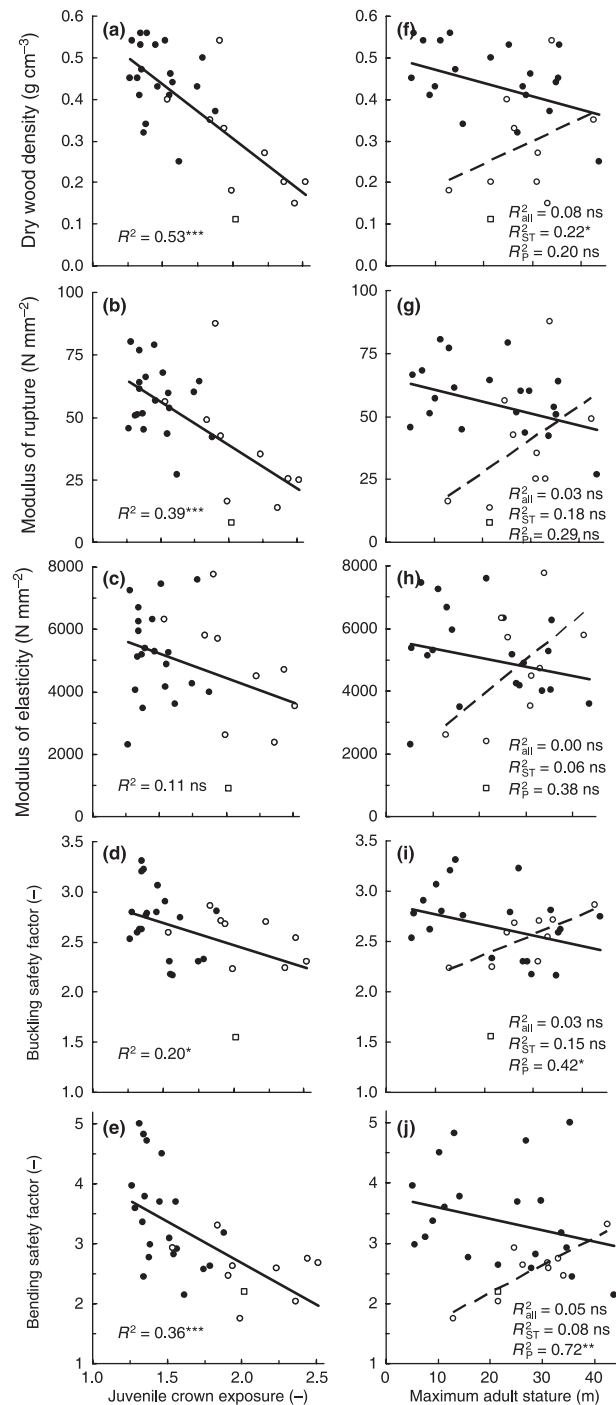


Fig. 4 Relationship of wood properties and mechanical safety with juvenile crown exposure (a–e) and maximum adult stature (f–j) of 30 rain forest tree species. (a, f) Dry wood density; (b, g) modulus of rupture; (c, h) modulus of elasticity; (d, i) buckling safety factor; (e, j) stem bending safety factor. For juvenile crown exposure, regression lines are drawn for all species pooled ($n = 30$). For maximum adult stature, separate regression lines are shown for shade-tolerant species (closed symbols, continuous line, $n = 20$) and pioneer species (open symbols, dashed line, $n = 10$). Coefficients of determination (R_{all}^2 for all species; R_{ST}^2 for shade-tolerant species; R_{P}^2 for pioneer species) and significance levels (ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$) are shown. *Jacaratia spinosa* is indicated by an open square.

Dry density was a better predictor than saturated or green density, probably because dry wood consists mainly of fibres, and fibres mainly determine wood strength (Kollmann & Côté, 1968). Green density was the weakest predictor, probably because of differences in the hydration status of the samples, as some were collected after rainfall and others after a period of drought.

We found hardly any studies that report on fresh wood densities or (fresh) moduli of rupture for saplings in a forest community. An exception is a study by Chu (1975), who reported that the MOR of fresh and dry wood increased with wood density across adult trees of 138 Malaysian timber species. In most studies, wood density data are reported for dry wood and for adult trees only. For the species included in this study, adult wood density data were also available (L.P., unpublished data). Adult dry wood densities are, on average, 0.19 g cm^{-3} heavier than sapling dry wood densities (paired t -test, $t = 13.1$, $P < 0.001$, $df = 29$), probably because for the saplings the bark was included in the density measurements, and because anatomical changes between juvenile and adult wood result in an increase in density. Nevertheless, there was a strong correlation between sapling and adult wood density ($r = 0.91$, $P < 0.001$, $n = 30$), indicating that species ranking in wood density is largely maintained during ontogeny. In the Bolivian tree community, the dry wood densities of saplings ranged from 0.11 to 0.58, and the corresponding wood densities of adult trees from 0.10 to 0.90 g cm^{-3} . This is comparable with wood density ranges reported for adult trees from Neotropical tree communities (min = $0.12\text{--}0.33$, max = $0.92\text{--}1.11 \text{ g cm}^{-3}$; Muller-Landau, 2004; Wright *et al.*, 2006). As large trees vary more than saplings in their wood densities, they are also likely to vary more in their mechanical properties, with potentially important consequences for architecture, growth and survival.

Safety factors and their underlying components

Safety factors for buckling (1.6–3.3) and bending (1.4–5.0) were well above 1, indicating that species maintained large safety margins against mechanical failure. Safety factors were close to those calculated for stems of understorey saplings using buckling theory (Sterck & Bongers, 1998; Gavin & Peart, 1999), and are below the (buckling) safety factors ≈ 4 for trees grown in open sites (McMahon, 1973; Claussen & Maycock, 1995). At first sight, such a heavy investment in mechanical safety appears to be strange, given the limited carbon gain of forest saplings. Yet not all potential loads are accounted for in the mechanical model: the buckling model neglects stem inclination and crown dimensions, and both models neglect dynamic loads by wind, rain and falling debris. Niklas (2000) argues that safety factors based on static loads are misleading because most healthy stems mechanically fail as a result of wind-loading, rather than from supporting their own weight. For saplings growing in the lower forest strata such wind loads are likely to be small, but the loads imposed by rain, falling debris or animal activity could be significant. Although the absolute values of safety

factors would decrease if these dynamic loads were included, the interspecific differences are likely to remain.

The safety factor for buckling was related positively to MOE and dbh, and negatively to wood density and height (Table 3; Fig. 2), in line with the buckling formula (equation 4). In principle, denser wood results in a heavier plant that would buckle more easily under its own weight. Wood density therefore has a direct negative effect on buckling safety through its mass, and a positive indirect effect through the MOE. Given the strong positive relationship between wood density and MOE (Fig. 1), it pays to invest in dense wood, as the MOE is a stronger determinant of the buckling safety factor than the wood density (Table 3). Interspecific differences in realized height had the largest effect on the buckling safety factor, indicating that tree architecture affects stability more than wood properties. Coexisting tree species vary tremendously in tree height when compared at the same dbh (Thomas, 1996; Sterck *et al.*, 2001; Poorter *et al.*, 2003, 2006), and trees with high height : diameter ratios have a high probability of snapping (Putz *et al.*, 1983).

Bending safety factors were larger for stems than for branches. The bending safety factors for stems may suffer more from overestimation than those for branches, as wind forces were not included in the calculations. Individual branches may minimize wind drag by aligning their leaves, and by swaying in the wind (Ennos, 1997). Stems typically resist the wind forces that act on the entire crown (Niklas, 1992; Mattheck, 1998), and may therefore be thicker than branches of the same length. The difficulty in calculating the contribution of wind to mechanical forces and safety margins therefore complicates a direct comparison between stem and branches (but see Henry & Thomas, 2002).

Bending forces were calculated from the applied load and moment arm, that is, the distance to the centre of mass of the attached distal structure. The resistance of stem and branches to these forces depends on MOR (break strength), saturated wood density and diameter. When the outlier *Jacaratia* was excluded from the analysis, the interspecific variation in the stem bending factor was explained mainly by the saturated wood density and stem diameter. As wind forces were not included, the stem safety factor resulted mainly from the relatively low compression forces. In contrast, the branch safety factor resulted mainly from the relatively high bending forces, because of their own mass and horizontal orientation. Although saturated density and MOR contribute equally to branch bending safety in physical terms, the across-species variation in branch bending safety was explained mainly by the MOR because the MOR varied 10-fold, while the saturated density varied only twofold.

Life-history variation: average juvenile crown exposure and maximum adult stature

We used CE_{juv} to rank the species based on their light requirements for regeneration. A low CE_{juv} indicates that

species regenerate mainly in the shaded understorey, whereas a high CE_{juv} indicates that species regenerate mainly in the bright light environment of gaps. Maximum adult stature was moderately correlated with CE_{juv} , indicating that taller species that spend a large part of their life in the canopy are also more light-demanding in the sapling stage (cf. Poorter *et al.*, 2006). When all species were combined, the wood traits and safety factors correlated significantly with CE_{juv} but not with maximum adult stature.

Juvenile crown exposure Wood density, MOR and safety factors for buckling and bending decreased with the CE_{juv} of the species (Fig. 4), in line with the hypothesis; but the MOE did not vary with CE_{juv} , in contrast to the hypothesis. Pioneer species, as a group, tend to have a low wood density compared with shade-tolerant species (Fig. 4a, cf. Swaine & Whitmore, 1988; Suzuki, 1999). A low wood density gives rise to fast height and diameter growth rates (Arets *et al.*, 2003; Muller-Landau, 2004; King *et al.*, 2005) because more stem volume can be constructed with the same mass of wood. Pioneers with high CE_{juv} grew at lower buckling safety margins, as did shade-tolerant species (Fig. 4d). This is in line with the results of other studies that suggest smaller safety margins for pioneers, but these studies evaluated too few species (two to four) to be able to draw firm conclusions (King, 1986; Claussen & Maycock, 1995; Sterck & Bongers, 1998).

Height was the main determinant of interspecific variation in safety for buckling. Large-scale community studies have shown that stem slenderness increases with the light requirements of the species (King, 1996; Poorter *et al.*, 2003), and that species with slender stems grow more efficiently in height, and have better access to light, than species with stouter stems (Poorter *et al.*, 2005). A low wood density (Fig. 4a) therefore gives pioneer species a key advantage in gaps, as they can grow rapidly and efficiently in height to outcompete their neighbours, and attain a position in the canopy before the gap closes.

Shade-tolerant species had a higher wood density and MOR, thus reducing the probability of physical damage caused by falling debris. Species that live in closed vegetation, such as shade-tolerant species, may suffer frequently from physical damage, and should be better adapted to such disturbances than pioneer species that occur in gaps. Indeed, it has been found that damage frequencies were higher in closed forest than in open areas (Gartner, 1989), and that shade-tolerant species experience higher damage rates than light-demanding species (Gartner, 1989; Putz & Brokaw, 1989; Paciorek *et al.*, 2000). Sapling survival of rain forest species is positively related to wood density (Muller-Landau, 2004; L.P., unpublished data), and the chance of stem breakage diminishes with an increase in MOR of the species (Putz *et al.*, 1983). Alvarez (2005) evaluated stem biomechanical traits and seedling survival in eight Panamanian tree species. Seedling survival in the shade was positively related to MOE, stem density and stem 'toughness', an equivalent of MOR. Stem density was the best predictor of survival, probably because it is closely related to resistance against physical damage (Fig. 1b)

and protection against fungi, which are important mortality agents in the seedling stage (Augspurger, 1984).

Wood properties and safety factors varied gradually and continuously with the CE_{juv} of the species (Fig. 4a–e). This suggests that 'pioneers' and 'shade-tolerants' are just two landmarks on a species continuum in shade tolerance. As both groups differ in their average CE_{juv} , they also tend to differ in their average trait values (Table 2).

Maximum adult stature Wood traits and safety factors did not correlate with maximum adult stature when all species were pooled. Other studies showed that many wood and architectural traits correlate with maximum adult stature, including wood density (Thomas, 1996; Falster & Westoby, 2004) and crown length and diameter (Sterck *et al.*, 2001; Kohyama *et al.*, 2003; Poorter *et al.*, 2003). Some studies (Thomas, 1996; Poorter *et al.*, 2003) included only shade-tolerant species, for which a strong relationship with maximum adult stature is expected, because tall species experience higher light levels over their lifetime, given the strong vertical light gradient in the forest canopy. For pioneer species, the relationship between adult stature and light demand is negative rather than positive, because early in succession small, highly light-demanding species are gradually replaced by taller, more shade-tolerant pioneer species.

The ANCOVA indicated that wood traits and safety factors of pioneer and shade-tolerant species showed opposite relationships to adult stature (Fig. 4). With an increase in maximum adult stature, the wood density, strength, stiffness and safety factors decreased for shade-tolerants, but increased for pioneers. Falster & Westoby (2004) found the same pattern for wood density in Australian rain forest species. Shade-tolerant species establish in a later phase of succession and partition the vertical light gradient in the forest. Short shade-tolerant species spend their whole lifetime under a closed forest canopy and have greater lifetime risks of being hit by falling debris. They therefore need denser, stronger and stiffer wood and more mechanical safety to survive in the understorey. Tall shade-tolerant species, on the other hand, escape size-dependent damage. With their low wood density and low safety margins, they grow rapidly and efficiently to the canopy to attain their large reproductive size. Pioneer species establish early in succession, where light availability decreases rapidly over time because of vegetation regrowth (Saldarriaga, 1994). Short pioneers dominate early in succession where growth is fast and competition for light is strongest. They therefore have a low wood density and grow at low safety margins to outcompete their neighbours. Tall pioneer species are also often longer-lived and need to invest in denser, stronger, stiffer wood and mechanical safety to be able to persist for a long time in the closing canopy.

Conclusions

This study is, to our knowledge, the first to show how differences in properties of wood affect the mechanical safety of saplings,

and how wood traits and mechanical safety correlate with life-history traits for a large set of species. There are large differences in wood density across coexisting species. Density is strongly positively related with strength and stiffness. Species' safety factor for buckling was positively related to wood density and stiffness, but tree architecture ($H:D$ ratio) was a stronger determinant of the safety factor than wood properties. Shade-tolerant species had dense, tough wood to enhance survival in the understorey, whereas pioneer species had weak wood and low safety margins to enhance growth in gaps. Our results support the idea that light demand and adult stature represent largely independent axes of variation (Turner, 2001), and that species differentiation along the vertical gradient differed between pioneer and shade-tolerant species (Falster & Westoby, 2004). These life-history axes affect wood properties, tree architecture and plant performance in different ways, thus contributing to the coexistence of rain forest tree species.

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