

# Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest

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## Summary

**1** Trade-offs among plant traits may contribute to specialization for different environments and coexistence of plant species. This may be the first study that shows how trade-offs among branch traits contribute to variation in crown size, light requirements and maximum height across multiple sympatric tree species in a tropical rain forest.

**2** Ten saplings were selected for each of 30 tree species in a Bolivian rain forest. Sapling height and crown dimensions were measured and branch and stem samples were harvested. Fresh density, dry density, modulus of rupture, centre of mass, biomass and diameters were determined for those samples. For each species, cantilever theory predicted the mass needed to produce a stable 1-m long horizontal branch.

**3** Generally, shade-tolerant species had denser and stronger branches, and produced a stable horizontal branch at lower resource costs. These species had branches with a higher resistance against mechanical failure, and a wide crown that favours effective light acquisition. Less shade-tolerant species had low density and weak branches, short branches, high resource costs per unit branch length, and low resource costs per unit stem length. These traits seem advantageous under conditions of prolonged exposure to direct sunlight, where such species grow rapidly to reproductive size, while mechanical risks are low and light levels are favourable.

**4** Branch (wood and bark) traits are good predictors for performance differences across tree species in heterogeneous forest light environments. Physical trade-offs among branch traits contribute to the specialization of tree species for different light habitats and to tree species coexistence in tropical rain forests, even within classical functional groups such as pioneers and shade tolerants.

*Key-words:* Bolivia, biomechanics, coexistence, crown form, diversity, maximum height, life history, safety factor, shade tolerance, tropical rain forest, wood density.

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## Introduction

One hypothesis to explain the coexistence of many tree species in tropical forests is that trade-offs among plant characters result in specialization for different light environments (Ricklefs 1977). In mature closed forest sites, short shade-tolerant species are expected to be specialized for low irradiance in the understorey, and tall shade-tolerant species for higher irradiance levels

in the forest canopy (Thomas & Bazzaz 1999). In open disturbed sites, short short-lived pioneers establish and grow rapidly and monopolize open sites (Finegan 1996), whereas taller long-lived pioneers grow slower and encounter some shading before they reach maximum height (Peña-Claros 2003). The basic working hypothesis for such specializations is that each species achieves the greatest net carbon gain (carbon acquisition rate minus losses due to respiration, turnover, herbivory) in a particular light environment (Givnish 1988). Earlier studies have shown how leaf trait trade-offs resulted in specialization for different light environments in tropical tree communities (Thomas & Bazzaz 1999; Poorter & Bongers 2006; Sterck *et al.* 2006). The role of stem

and branch trade-offs in such specialization remains little understood (van Gelder *et al.* 2006). In this study, branch traits were investigated to explain variation in crown size, light requirements and maximum height across tree species that coexist in tropical rain forests.

Because light is a limiting resource in the forest understorey, understorey saplings partition more resources to leaves, at the expense of non-leaf tissues (King 1991; Poorter 2001). Consequently, trees may grow close to minimum mechanical safety, and produce relatively slender stems (Sterck & Bongers 1998) and branches (Pearcy *et al.* 2005). Cantilever beam theory (Gere 2004) predicts the mechanical forces acting on a horizontal free hanging structure, and can be used to calculate the minimum investments needed to prevent branches from rupture due to their mass. Theoretical predictions on branch shape were supported for temperate conifers (Morgan & Cannell 1987, 1988) and for saplings of tropical tree species (Pearcy *et al.* 2005). The mass invested in a stable branch axis is expected to vary with branch size, branch shape and branch axis density. Because these properties strongly vary across species (shape, Hallé *et al.* 1978; Valladares *et al.* 2002; wood density, Reyes *et al.* 1992; Niklas 1993; bark properties, Niklas 1999; and size, Sterck *et al.* 2001; Poorter *et al.* 2003, 2006), species potentially differ in the mass needed to produce a particular branch and crown size (King *et al.* 2006). In this study, cantilever theory and branch traits were used to predict the minimum radius and mass needed to produce a stable horizontal branch in saplings of 30 sympatric tree species. Subsequently, the mass investments in such a branch were related to interspecific variation in crown width, maximum height and light requirements.

This study may be the first that uses a comparative data set for a large number of sympatric tree species to upscale mechanical branch constraints to interspecific variation in branch traits and crown size, and to evaluate the consequences of this for the light requirements and maximum height of the species. The following questions were addressed. (i) How do branch traits influence the interspecific differences in mass needed to produce a stable branch? (ii) How do differences in this stable branch mass explain the variation in crown size, light requirements and maximum height among species? The across species analyses were performed for 30 sympatric tree species of a Bolivian tree community. Ten pioneer and 20 shade-tolerant species were selected, to analyse whether the same patterns are found within functional groups as between functional groups. We discuss how branch trait variation across species contributes to specialization for high- and low-light environments.

## Materials and methods

The study was performed in the La Chonta forest, Bolivia (15°47' S, 62°55' W). The forest can be classified as a lowland tropical moist forest. Forests are situated

on an extension of the Brazilian Shield. Mean annual precipitation is 1520 mm, mean temperature is 25.3 °C, and the dry season lasts from May until October. Approximately one-third of the canopy species are deciduous during the dry season. Thirty tree species were selected for this study. Species were classified into 10 pioneer species that require high-light intensities for successful regeneration, and 20 shade-tolerant species that can establish and survive in the shade (Poorter *et al.* 2006). These species are among the most common species of the forest, and were easily recognized by experienced tree spotters. For species details, see van Gelder *et al.* (2006).

Poorter *et al.* (2006) estimated the height and crown exposure (cf. Dawkins & Field 1978) for 662 (range 41–9319) individuals per species. The crown exposure varied from 1 when a tree did not receive direct light, 2 when it received lateral light, 3 when it received overhead light to part of the crown, 4 when it received full overhead light to the whole crown, and 5 when it had an emergent crown that received light from all directions. Crown exposure relates strongly to canopy openness (Davies *et al.* 1998). For each species, crown exposure was related to tree height, using a multinomial regression analysis (cf. Poorter *et al.* 2005; Sheil *et al.* 2006). The average crown exposure for a 2-m tall sapling is referred to as juvenile crown exposure (Poorter *et al.* 2006; van Gelder *et al.* 2006). Predicted maximum height was calculated for each species using the diameter for the third thickest tree in 320 ha of permanent sample plots in La Chonta (Instituto Boliviano de Investigación Forestal, unpublished data) and species-specific, height-diameter relationships (Poorter *et al.* 2006).

For each species, five individuals growing under low light conditions (occurring in complete shade or receiving an intermediate amount of direct lateral light; crown exposure < 2.5, Clark & Clark 1992) and five individuals growing under high light conditions (receiving a high amount of direct lateral light, or overhead light to the crown; crown exposure ≥ 2.5) were randomly selected. Low- and high-light exposure individuals did not differ in branch properties, and were therefore pooled per species in the further analyses (van Gelder *et al.*, unpublished data). Crown position index of the selected saplings did not differ significantly among species. Sapling height ranged between 1.8 m and 4.0 m (mean = 2.3 m), and diameter at breast height (d.b.h.) between 5.9 mm and 36.5 mm (mean = 17.8 mm).

Besides height (precision *c.* 1 cm) and d.b.h. (*c.* 0.5 mm), crown width (*c.* 1 cm), length (*c.* 1 cm) and angle (*c.* 1°) of the largest branch were measured for each sapling. The branch was then cut to measure its length, diameter at 5 cm from the base, fresh mass (including leaves), and the centre of mass. The centre of mass was determined by balancing the branch horizontally on a pencil. Stem/branch axis properties were determined using six axis samples from each individual, taken at different positions: two from the lowest branch, two from the stem base, and two from the terminal metre of

the stem. Samples were visually selected for being free of notches and bark disturbances, and for having a straight axis and a circular cross-section area. The sampled axis that were used for further analysis included both wood and bark, since both wood and bark are expected to contribute significantly to the mechanical traits of stem and branches in saplings (Niklas 1999). Fresh volume, fresh mass and dry mass were measured for each axis, and hardly differed between axes taken from different positions. Using sample length and thicknesses at the lowest and highest point, fresh volume was calculated approximating the shape of a truncated cone. Fresh mass was measured on the day of collection. Samples were dried for 4 days at 70 °C and then reweighed to obtain dry mass. Basic axis property data are presented elsewhere (van Gelder *et al.* 2006).

Fresh and dry densities were calculated from the branch samples. The modulus of rupture was measured on the fresh sample from the stem base with a diameter of about 20 mm. For testing the modulus of rupture, samples were used that had a length/thickness ratio of 18 and a span-length/thickness ratio of 15 (Kollmann & Côté 1968). The modulus of rupture was determined in a three-point bending test using a four-screw type loading device (manufacturer Tinius Olsen, Horsham, USA; model 62; calibrated to the ASTM E4 standard; a class A device; accuracy is 1% of the applied load). The specimen in bending was horizontally placed on two supports with span length  $L$ . At the midpoint of the specimen, a vertical, downward-orientated load was applied and augmented by increasing the vertical midpoint deflection of the specimen at a known vertical, downward-orientated speed. The vertical midpoint deflection was recorded for each load interval of 2.5 kg, until the maximum load was reached (mean test time 3 min; deflection speed varying between 1.5 mm s<sup>-1</sup> and 3 mm s<sup>-1</sup>). The formula for the modulus of rupture (MOR) of a two-side supported sample with a circular cross section is:

$$\text{MOR} = (M_{\text{max}} \cdot z)/I = (1/4 P_{\text{max}} \cdot L \cdot R)/(1/4 R^4)$$

where  $M_{\text{max}}$  is the maximum bending moment,  $I$  is the second order moment of area,  $z$  is the section modulus as the distance between the centre of a cross section and the outermost fibre,  $P_{\text{max}}$  is the maximum load,  $L$  the span-length, and  $R$  the radius. In a circular cross section  $z = R$  and  $I = 1/4\pi R^4$  (Gere 2004).

The bending model predicted the minimum possible or self-supporting diameter ( $D_{\text{min}}$ ) of branches as one-side supported cantilevers.  $D_{\text{min}}$  was derived from the formula for applied bending stress  $\sigma$  on a circular cross section with a known own self-load ( $P$ ), bending moment ( $M$ ), and horizontal arm length  $L_{\text{cm}}$  to the centre of mass.

$$\sigma = (M \cdot z)/I = (P \cdot L_{\text{cm}} \cdot R)/(1/4\pi R^4) \leq \text{MOR} \text{ and } D_{\text{min}} = 2R$$

Although this method does neglect significant loading due to rain and wind loads, it was considered to be a

valid tool to compare branches across species. The safety factor  $S$  against bending forces due to self-load is the ratio of the observed to predicted minimum diameter,

$$S = D_{\text{obs}}/D_{\text{min}}$$

This safety factor has been used in the ecological literature (e.g. van Gelder *et al.* 2006), but typically scales with the cube of the safety factor used by engineers (breaking stress/maximum expected stress). To compare branch masses, the mass in a hypothetical horizontal branch cylinder of 1 m length was estimated. The hypothetical branch cylinder excluded leaves and side branches, and thus simplified the branch to a linear axis. Because this means that the mass load was relatively low, the hypothetical branches were thinner than actual branches. The parameters for a hypothetical branch, however, provided comparative data to contrast the consequences of different branch axis properties for branch axis dimensions and, ultimately, for the mass in a 1-m horizontal branch length with a minimum branch diameter (i.e. a safety factor equal to 1). Mechanical theory predicts the minimum diameter at the base of such a hypothetical branch as,

$$D_{\text{min}'} = (4L2\rho_{\text{sat}} \cdot g)/\text{MOR}$$

With the length of the branch ( $L = 1$  m), the fresh branch axis density  $\rho_{\text{sat}}$  (g cm<sup>-3</sup>), the modulus of rupture MOR in N mm<sup>-2</sup>, and the gravity constant  $g$ . The diameter of that hypothetical branch was calculated from the actual branch safety factor  $S$ ,

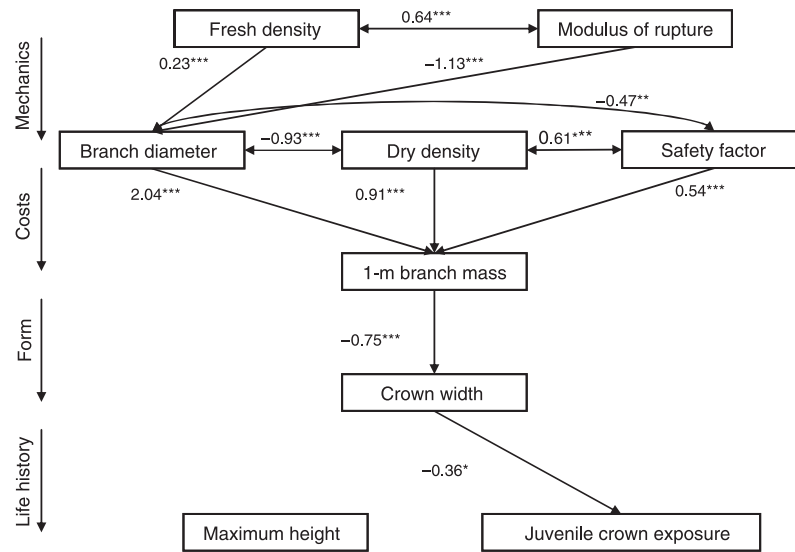
$$D = S \cdot D_{\text{min}'}$$

Branch mass ( $C$ ) was calculated as the dry biomass that was needed to produce the hypothetical branch cylinder,

$$C = 1/4\pi D^2 L \rho_{\text{dry}}$$

Branch mass depended on the branch diameter,  $D$ , length,  $L$ , was set at 1 m, and the dry branch axis density,  $\rho_{\text{dry}}$ .

The 30 tree species were compared for the influence of (i) fresh branch axis density and modulus of rupture on the minimum diameter of a hypothetical branch of 1 m (mechanics); (ii) the minimum branch diameter, dry branch axis density and safety factor on branch mass (investment); (iii) branch mass on crown width (form); and (iv) crown width on juvenile crown exposure and maximum height (life history). Bivariate relationships were analysed using a Pearson correlation. A path analysis distinguishes the direct vs. indirect effects (through correlation with other factors), and compares the contributions of different predictors (Sokal & Rohlf 1995). Log-transformation was necessary to meet the assumptions of an additive regression model. The analyses were performed for all pooled species, and for shade-tolerant and pioneer species considered separately.



**Fig. 1** A path-analysis diagram is shown for relationships between branch, crown, and life-history traits across 30 species in La Chonta, a Bolivian rain forest. The double headed-arrows represent correlations and are accompanied by (bivariate) Pearson correlation coefficients. Single-headed arrows represent causal relationships and the figures are the standardized regression coefficients of the multiple regressions of the predictors on the dependent variable. \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , and \* $P < 0.05$ .

**Table 1** Branch design and life history values for pioneer ( $n = 10$ ) and shade-tolerant ( $n = 20$ ) species. The values are based on a sample of 10 individuals per species

Traits	Units	Pioneers		Shade tolerants	
		Mean	Range	Mean	Range
Dry branch axis density	$\text{g cm}^{-3}$	0.29	0.11–0.56	0.46	0.25–0.58
Fresh branch axis density	$\text{g cm}^{-3}$	0.86	0.66–1.07	1.01	0.78–1.10
Modulus of rupture	$\text{N mm}^{-2}$	35.8	7.6–87.6	57.3	26.9–80.3
Safety factor	$\text{mm mm}^{-1}$	1.56	1.43–2.03	2.12	1.75–2.12
Minimum 1-m branch diameter	mm	1.61	0.53–4.90	0.79	0.53–1.28
1-m branch mass	$\text{g m}^{-1}$	1.52	0.47–6.12	1.01	0.56–1.63
Crown width	m	1.47	1.00–2.09	1.52	1.09–1.94
Juvenile crown exposure	–	2.35	1.50–4.00	1.69	1.38–2.07
Maximum height	m	24.9	12.7–31.7	21.0	5.1–41.2

## Results

Branch axis properties and branch shape were related to life-history variation among species in four steps (Table 1, Fig. 1). The effects of fresh density and modulus of rupture on the minimum branch diameter for the support of a 1-m long horizontal branch axis were analysed. The minimum branch diameter was mainly determined by the modulus of rupture; as expected, species with a large modulus of rupture needed only thin branches to prevent bending (Table 2, Fig. 2b). Path analysis revealed that fresh density had a direct positive direct effect on the minimum branch diameter (Fig. 1). However, due to the strong positive correlation with the modulus of rupture, it had a large negative indirect effect on the minimum branch diameter, resulting in a negative correlation between the fresh density and the minimum branch diameter (Fig. 2a). Similar relationships were found when pioneer species and shade-tolerant species were analysed separately (Sterck

*et al.* unpublished results), except that pioneers had a slightly lower minimum branch diameter for a given modulus of rupture (Fig. 2b, Table 2).

As expected, the diameter, dry density and safety factor positively affected the mass that was needed to form a stable 1-m long horizontal branch axis. Minimum diameter had a stronger positive effect on the branch mass than dry density or safety factor (Fig. 1). Dry density correlated negatively with branch mass (Fig. 2d) due to the strong negative indirect effects via its correlation with minimum diameter (Fig. 1). These relationships held when shade-tolerant species and pioneer species were analysed separately (F. J. Sterck, unpublished data). Pioneers, however, had a lower branch mass than shade tolerants for the same dry density (Fig. 2d, Table 2) due to a lower safety factor, and for the same branch diameter (Fig. 2c, Table 2) due to a lower dry density.

Branch mass had a negative effect on the crown width (Figs 1 & 2f) and, in turn, crown width related

**Table 2** Results of a multiple regression model.  $\log(y) = a + b \log(x) + c \cdot \text{dummy} + d \log(x)\text{dummy}$ . The latter is the interaction (int.) term. The dummy is 1 for pioneers and 0 for shade tolerants. For units see Table 1

	<i>x</i>	<i>y</i>	<i>a</i>	<i>b</i>	<i>c</i>	Int.	<i>R</i> <sup>2</sup>	<i>n</i>
1	Modulus of rupture	Minimum branch diameter	1.513***	-0.908***	-0.043*	n.s.	0.97	30
2	Fresh density	Minimum branch diameter	-0.080*	-1.800**	n.s.	n.s.	0.24	30
3	Minimum branch diameter	1-m branch mass	0.307***	1.049***	-0.200***	n.s.	0.83	30
4	Dry density†	1-m branch mass	1.685***	-1.473(*)			0.18	20‡
			3.952*	-8.197(*)			0.43	10§
5	Safety factor	1-m branch mass	n.s.	n.s.	n.s.	n.s.		30
6	1-m branch mass	Crown width	1.514***	-0.837***	n.s.	n.s.	0.52	30
7	Crown width	Juvenile crown exposure	0.216***	-0.275*	0.141***	n.s.	0.66	30
8	Crown width	Maximum height	n.s.	n.s.	n.s.	n.s.		30

\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , (\*) $P < 0.10$ ; n.s., not significant.

†As interaction term was significant ( $P = 0.035$ ), results are shown for pioneers and shade tolerants separately, using  $\log(y) = a + b \log(x)$ .

‡Shade tolerants.

§Pioneer.

negatively to juvenile crown exposure (Figs 1 & 2g). These patterns held for pioneers and shade tolerants separately (F.J. Sterck *et al.*, unpublished data). For a given crown width, however, pioneers had a higher juvenile crown exposure than shade-tolerants. (Table 2, Fig. 2g). No significant relationships were found between crown width and maximum height (Fig. 2h).

## Discussion

The 30 tree species were compared for the influence of mechanical constraints and branch traits on the mass needed to produce a stable horizontal branch and, in turn, on the crown width, light requirements and maximum height of the species. Our results suggest why species with thick, short, weak and expensive branches had narrower crowns and occupied more open habitats than other species. Support was found for the idea that branch traits and mechanical constraints contribute to specialization between and within the pioneer and shade-tolerant guilds.

### MECHANICAL CONSTRAINTS AND THE MASS OF A STABLE HORIZONTAL BRANCH AXIS

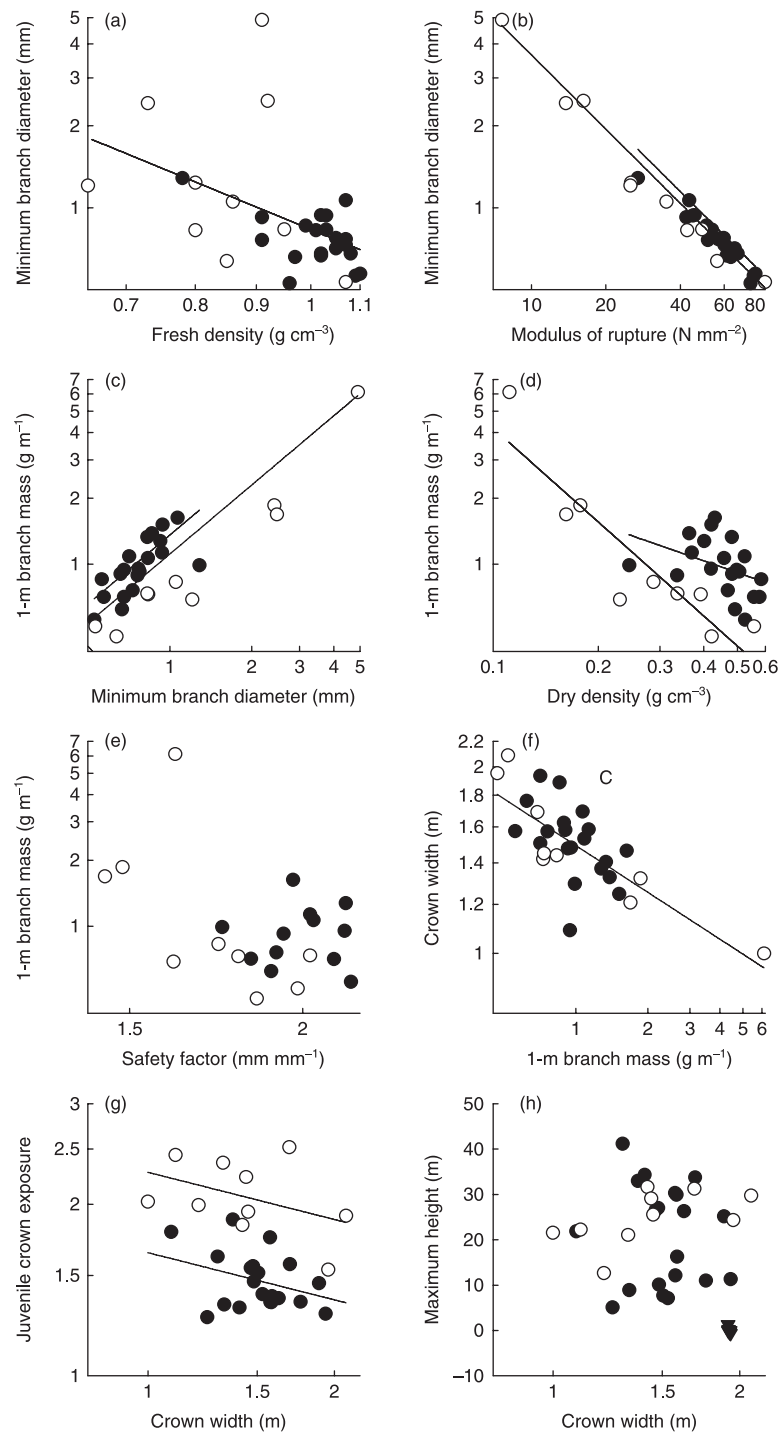
According to cantilever beam theory, the minimum branch diameter is proportional to the quotient of the fresh branch axis density to the modulus of rupture. We did not find other studies that compare (fresh) density and modulus of rupture for saplings of multiple species in the same forest community (for dry wood density comparisons within and across tropical tree communities, see Muller-Landau 2004). In the La Chonta forest, the modulus of rupture varied by a factor of  $> 10$  across species (range 8–88 N mm<sup>-2</sup>), whereas fresh density only varied by a factor of  $< 2$  (range 0.66–1.10 g cm<sup>3</sup>). Consequently, the minimum branch diameter was more strongly correlated with the modulus of rupture across the 30 species than with fresh density (Figs 1 & 2a,b). These trends held when analysed for all species pooled, and when pioneer species and shade-tolerant

species were considered separately. Given the strong physical relationship between density, modulus of rupture and minimum branch diameter, it was surprising that pioneers had a lower minimum branch diameter for the same modulus of rupture. A quantitatively more significant difference between the two groups is that the five species with the lowest modulus of rupture were pioneers that had considerably larger minimum branch diameters than 19 out of 20 shade-tolerant species (Fig. 2b). Van Gelder *et al.* (2006) showed that pioneers on average had a lower modulus of rupture than shade tolerants. Note, however, that the other five pioneers covered the same range of modulus of rupture as those of 19 out of 20 shade-tolerant tree species (Fig. 2b). The variation in these mechanical properties and minimum branch diameter is thus much larger across pioneer than shade-tolerant species.

The path-analysis showed that the large effect of the modulus of rupture on the minimum branch diameter mainly determined the interspecific variation in the branch mass that is needed to produce a stable horizontal branch. Dry density and safety factor had minor effects on this branch mass. Strikingly, these effects differed quantitatively between the pioneers and shade tolerants. At the same minimum diameter, pioneers had a lower branch mass than shade tolerants. The lower safety factor and lower dry branch axis density for the pioneer species (Fig. 2e) may contribute to this difference.

### BRANCH AXIS TRAITS AND LIFE-HISTORY VARIATION

No relationship was found between crown width and maximum height; neither for all species pooled nor for pioneers and shade tolerants considered separately. Poorter *et al.* (2006) also found few relationships between architectural traits and maximum height in the same community. These weak relationships between crown size and maximum height contrast with the results for tree communities from wetter and taller forests, showing that shorter-stature species have wider crowns than



**Fig. 2** Bivariate relationships between different plant traits across 30 tree species in La Chonta, a Bolivian rain forest. Pioneers ( $n = 10$ ) are represented as open dots, and shade-tolerants ( $n = 20$ ) as filled dots. The regression lines correspond with the multiple regression analyses, as presented in Table 2.

larger-stature species (Sterck *et al.* 2001; Poorter *et al.* 2003). Poorter *et al.* (2006) speculated that the lack of such patterns in La Chonta resulted from the relatively low, open, semi-evergreen canopy of this forest. Such a canopy results in more light penetration, a weaker vertical light gradient, and thus in a smaller difference in the light environment of short- vs. tall-stature species.

Crown size and shape set the limits to the leaf display (Horn 1971; Kohyama & Hotta 1990; Sterck *et al.* 2001)

and, in turn, leaf display determines to a large extent the light interception and whole-plant carbon gain (Warren-Wilson 1981; Pearcy & Yang 1996; Sterck *et al.* 2005). Our results show that species differed in the branch mass needed to produce a stable horizontal branch by a magnitude of more than 10. The branch mass differences were negatively related with crown width across the species. How do these branch costs relate to the costs of producing 1-m stem? To explore

this question the mass in the horizontal 1-m branch axes was related to the measured mass in the last meter of the stem axis. Branch and stem mass were negatively correlated (on  $\log_{10}$  transformed values, branch vs. stem mass, Pearson's  $R = -0.63$ ,  $P < 0.001$ ,  $n = 30$ ). Moreover, the 1-m stem mass was negatively associated with our species' light-requirement measure, i.e. the juvenile crown exposure (stem mass [ $\log_{10}$  transformed] =  $2.2 + -0.28 \times$  exposure;  $R^2 = 0.60$ ,  $P < 0.000$ ,  $n = 30$ ). This means that species with strong, dense and thin branches produced relatively cheap branches, wider crowns, but with an expensive stem. These species occurred in more shaded conditions and may facilitate leaf display over a wider area to avoid self-shading. In contrast, species of more open environments produced a cheaper stem and relatively expensive short branches. The high water conductivity of species with low density wood and wide stems may enable such species to maintain high assimilation rates and high growth rates in the meristems (Tyree & Zimmermann 2002). Consequently, these species may thus grow rapidly in height towards reproductive size.

These results suggest how mechanical constraints contribute to specialization for different light environments, and to the pessimist vs. optimist strategy as observed in other tree communities (Aiba & Kohyama 1997). The patterns were strong, did not depend on outliers, and appeared both within the pioneer and shade-tolerant guilds. This suggests that the variation in coupled branch axis traits acts as a trade-off, and provides ample opportunity for specialization to light and associated factors.

The large variation in the branch design of pioneers is paralleled by the large variation in leaf traits, growth rate, survival rate, life span and juvenile crown exposure of pioneers in the same Bolivian tree community (Poorter & Bongers 2006; Sterck *et al.* 2006). The same has been found for other tree communities (Veneklaas & Poorter 1998). Pioneer species with the most extreme light and weak branches are specialized for a short life in fully exposed conditions. The most extreme species in this respect are *Jacaratia spinosa*, *Heliocarpus appendiculatus* and *Urera caracasana*. These so-called short-lived pioneers produced short and short-lived branches, and allocated a larger fraction of their resources to vertical stem extension than to horizontal branch extension. The low stiffness and strength across the grain may also limit the ability of stems to support large branches in such species. Such limitations for lateral expansion, however, do not hinder their ability to win the height race for the canopy and complete their life cycle rapidly. The so-called long-lived pioneers are at the other extreme in this group: they produce more stable, cheaper, branches and a wider crown, and they grow slower (in height) and occur at less exposed conditions than the rapid, short-lived pioneers (Poorter *et al.* 2006., Finegan 1996; Peña-Claros 2003). Unlike short-lived pioneers, they may survive for some time during gap closure. Because of their stronger branches, they are better able than shorter-lived pioneer trees to withstand the

higher risks of damage by liana loads (Schnitzer *et al.* 2000) and falling branches and stems. Ultimately, at the population level, the high mortality rate (e.g. due to mechanical failures) of the short-stature pioneers may be compensated for by their rapid attainment of reproduction. In contrast, the longer-lived pioneers take more time to reach a reproductive state, but they have better rates of survival along the way.

Shade tolerants establish in shaded conditions, grow slowly, and may spend many years before they become reproductive (Thomas 1996). The relatively small variation in branch design properties in this large species pool suggests important constraints on branch traits of shade-tolerant species. There may be various reasons for the narrow range of dense and strong branches in the shade-tolerant group, e.g. the resistance of dense wood against mechanical failure (Alvarez-Clare 2005), rot and diseases (Augspurger 1984). Despite the relatively small variation in branch traits, the shade tolerants exhibited the same range of crown width variation as the pioneers (Fig. 2g), and showed differentiation for different light habitats in the forest. From this it was inferred that the longer route to reproduction and the higher risks of mechanical failure in shade conditions selected for convergence of branch traits among shade-tolerant species. In contrast, a broader range of light levels and mechanical risks in open gaps vs. closing gaps resulted in more divergence of branch traits among pioneer species. The variation of coupled branch traits seems sufficient to accommodate specialization to different light conditions within each group.

Pioneers and shade tolerants showed similar qualitative patterns among traits, but the quantitative relationships were sometimes different. The strongest difference was observed in the crown width–juvenile crown exposure relationship. For the same crown diameter, pioneers occurred at much more exposed light conditions than did shade tolerants. This group difference cannot be explained from the presented branch properties alone. Alternatively, leaf turnover rates and leaf and stem respiration rates may play a role here (Veneklaas & Poorter 1998; Sterck *et al.* 2006), but these were beyond the scope of this study.

## Conclusion

For 30 sympatric tree species in a Bolivian tree community, mechanical constraints and branch traits were scaled to the mass needed to produce stable horizontal branch of 1 m in length. This branch mass was related to the interspecific differences in crown size, light habitat and maximum height. Species of more shaded conditions had denser, stronger and cheaper branches, they better resisted mechanical forces, and they produced a wide crown favouring effective light acquisition. Species of more exposed light conditions had lighter and weaker branches, produced horizontal branches at higher costs, and allocated more resources to height growth. These properties seem advantageous under conditions

of more persistent exposure, where light levels are more favourable, change faster and mechanical risks are smaller. Moreover, low-density pioneers may be more efficient at resisting the larger wind forces in exposed sites, because more material is located further from the centre of the cross section of a branch or stem (Ennos 1997). Such wind forces were however, beyond the scope of the presented study.

The considerable variation in the data suggests that individual species may deviate from the overall patterns, and that factors other than mechanical constraints also contribute to crown form and life-history variation. Nevertheless, strong support was found for the idea that the physical coupling among branch traits acted as a trade-off that resulted in specialization for different light habitats, both between and within functional groups, and thus may contribute to the coexistence of tree species in tropical forests.

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