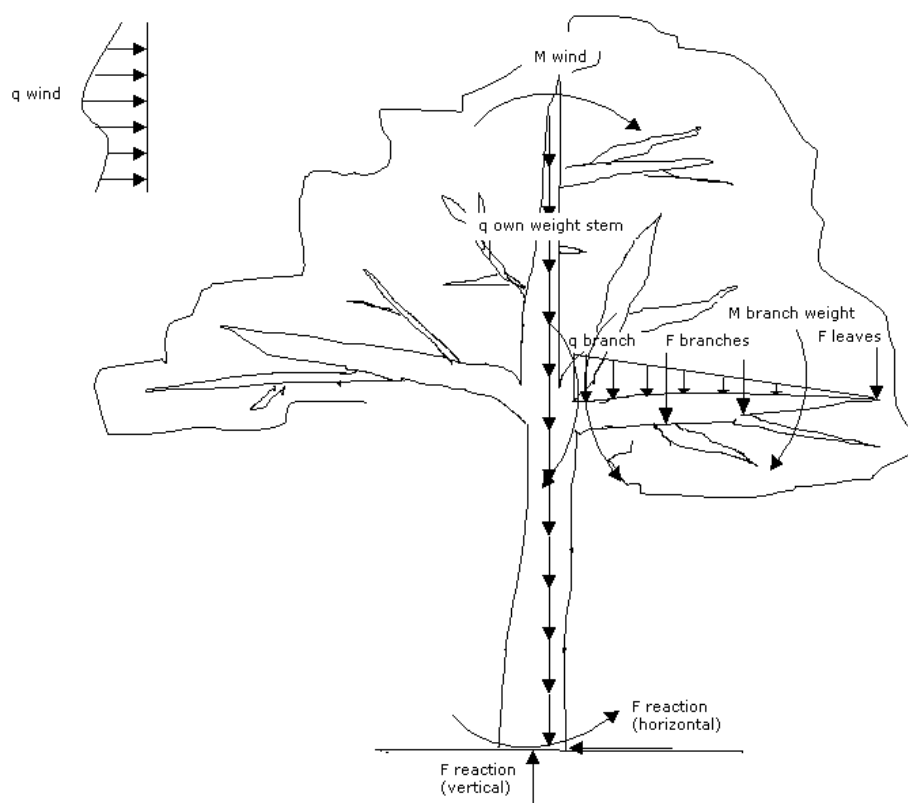


# Mechanical properties of tropical rain forest tree species and their consequences for crown development

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AV 2005\_43

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## Abstract

Plants have evolved different plant strategies and morphological and physiological traits to perform best under prevailing environmental conditions. Tree species show large differences in mechanical wood properties and tree architecture. A tree's architecture determines a tree's light capture, stability and efficiency of crown growth. In the understorey of moist tropical rain forests, irradiance is the most limiting resource for tree growth. In the limited light conditions of the understorey plants are expected to maximise light capture in the most efficient way, minimising construction and maintenance costs. A tree has to withstand all loads acting on it. Therefore, stems and branches have to grow strong enough. Saturated wood density acts as own weight load, and dry density indicates support costs. Wood strength gives a stem or branch the ability to withstand loads. The bending strength (Modulus of Rupture MOR), the compression strength (CS) and the stiffness (Modulus of Elasticity MOE) were studied. Global failure or breakage of a stem under a compressive load is called buckling. A more local phenomenon for stems and branches is bending, resulting in bending stresses. The aim of this research is to compare the wood properties of 30 rain forest tree species and 4 guilds along a successional gradient (shade-tolerant, partial shade-tolerant, long-lived pioneer and pioneer). Furthermore, what the consequences of wood properties are for mechanical safety factors, crown development and maximum adult stature.

Wood density was a very good predictor for wood strength and stiffness. With increasing density the strength increased, as did the stiffness. Horizontal branches had a higher dry wood density than vertical stems, but horizontal branches had a lower green and saturated density than vertical stems. This could be explained by vertical stems being relatively more important for transportation of water and nutrients. Consequently, vertical stems have more and/or larger vessels than horizontal branches. Wood density and strength decreased along the successional gradient going from shade-tolerant to pioneer species. The buckling- and bending safety factors differed significantly between species. The buckling safety factor differed almost significantly between guilds. The trend seemed a decrease in buckling safety factor going from shade-tolerant to pioneer. Pioneers with a rapid height growth seemed to have a lower safety factor to cut down height extension costs. Shade-tolerants seemed to have a higher safety factor for survival advantages in the understorey, reducing the risk of damage from falling debris and fungal infection. No trend was discovered for the bending safety factor. It could be that, compared to shade-tolerants, pioneers maintained a same level of safety, but minimising bending loads with different branching patterns, e.g. more upward orientation, less lateral branches or laterals positioned closer to the base of the main branch.

The horizontal branch growth costs were calculated for a horizontal branch with 1 m length and were based on biomechanics, wood density and strength. Horizontal branch growth costs differed significantly between species, not between guilds. Within the pioneer guild two different strategies for branch growth economy were found. Half of the pioneers grew horizontal branches at low costs, the other half at high costs. An increasing average juvenile crown exposure was correlated to branch growth costs ( $P=0.05$ ). Species experiencing higher light levels (pioneers) seemed to have higher costs for horizontal branch growth than species in lower light (shade-tolerants). Having higher branch growth costs resulted in less horizontal branches, but this trend was mainly caused by 3 deviating species, i.e. *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus*. Horizontal branch growth costs were negatively correlated with crown width. This trend was found with and without the 3 species mentioned above. High costs led to less wider crowns. It seemed that species specialised in rapid vertical stem extension at the cost of lateral crown growth. The maximum adult stature could not be correlated to wood density, strength or safety factors, when all species were pooled. However, subdividing the species in 2 groups, (partial) shade-tolerant vs. (long-lived) pioneer group resulted in opposing correlations. For the shade group the trend was that wood density, strength and safety factor decreased, when maximum adult stature increased. The pioneer group showed the exact opposite: wood density, strength and safety factor increased, when maximum adult stature increased. Light demand requires rapid height growth with low construction costs to reach or maintain in the canopy. Larger adult stature species need to grow to reach their reproductive size. So, light demand and adult stature represent 2 independent axes of differentiation, influencing the architecture and crown development of a tree.

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## Introduction

Plants have evolved different plant strategies to perform best under prevailing environmental conditions. The set or collection of traits in groups, syndromes or taxa can be considered as plant strategies. (Reich *et al.* 2003). Plant strategies are also named as functional groups or syndromes. A species has evolved a specific set of traits, *e.g.* light demand, drought tolerance. With this combined set of traits, the plant strategy, a species has adapted to prevailing environmental conditions to perform best, *e.g.* reproduction, regeneration or survival performance. In forests, strategies often relate to light requirements of the species. Light-demanding and/or pioneer species are species that need a high light environment, *e.g.* a gap, for establishment, whereas shade-tolerant, climax and/or non-pioneer species can germinate, grow and survive under low light conditions, *e.g.* the forest understorey (Hawthorne 1993; Swaine and Whitmore 1988; Whitmore 1989). Plants have developed several morphological and physiological traits that serve their strategy best. The “fit” of organisms to their environment reflects the adaptive value of plant functional traits (Ackerly 2003). Functional traits are biological characteristics of plant species that enhance their fitness, *i.e.* their growth or survival and ultimately reproduction. These traits determine how species compete for light, water and nutrients and when and under what conditions they regenerate.

In the understorey of moist tropical rain forests, irradiance is the most limiting resource for tree growth (Whitmore 1996). In the limited light conditions of the understorey plants are expected to maximise light capture in the most efficient way, minimising construction and maintenance costs (Givnish 1988). A tree’s architecture determines a tree’s light capture, stability and efficiency of crown growth (Poorter *et al.* 2003). Crown architecture design and optimisation is complex, fulfilling multiple functions and undergoing multiple constraints (Percy *et al.* 2005). The main functions of crown architecture are maximising whole-plant light capture and carbon gain, competitive ability and reproduction, while at the same time minimising damage risk and avoiding light and temperature stress and hydraulic limitations. Multiple constraints affecting crown architecture are biomechanical, hydraulic, developmental and allocational. Investment in sufficient biomechanical support and hydraulic sufficiency of stems is costly, resulting in less leaf area and less light capture. Developmental constraints, *e.g.* phyllotaxy, constrain the way resources can be allocated (Percy *et al.* 2005). Constraints imposed by other crown functions than light capture efficiency, such as hydraulics and biomechanical support may place upper limits on light capture efficiency (Percy *et al.* 2004).

The tree stem and crown support the photosynthetic apparatus and provide a good position of the leaves to the light with respect to neighbouring trees. The capture of light by plants depends on the amount and spatial distribution of radiation and the architectural arrangement of leaves within the plant’s crown (Percy *et al.* 2004). There is a trade-off between height growth required to take advantage of the strong vertical gradient of light availability in the understorey and the lateral crown extension needed to minimise self-shading of leaves and to forage for light (Kohyama and Hotta 1990). Branching pattern affects the leaf display efficiency (Valladares *et al.* 2002) and is approximately stationary within a species. Thus, individuals of a species show a similar branching pattern (McMahon and Kronauer 1976). Shade-tolerant *Psychotria* species have adapted in such a way that their light capture efficiency is slightly higher than light-demanding species (Percy *et al.* 2004). But in general the light capture efficiency is very similar despite the contrasting crown architecture and leaf habit (Valladares *et al.* 2002). So, with species having a similar total light capture, it could be that biomechanical constraints result in differences in light capture efficiency between species. For example King (2005) argues that differences in support costs are an important cause of observed interspecific differences in height growth rate. Poorter *et al.* (2003) suggest that the key factors driving interspecific differences in tree architecture are the costs of height extension and mechanical stability.

Carbon is one of the basic structural components for wood formation. The amount of carbon available for growth and maintenance depends on the photosynthetic capacity and the respiration. The carbon budget of a tree is restricted: for example carbon invested in wood cannot be invested in leaves. This is a so called trade-off.

The mechanical properties of wood vary strongly 1) between species (Tsoumis 1991; Kollmann and Côté 1968); 2) within species, for example phenotypic plasticity in wood density occurs for different light conditions (Igboanugo 1990); and 3) even within one individual, depending on the size, age and physiological condition of the plant (Niklas 1993a & 1997). Studies on mechanical properties, structural growth and architecture of trees have been done focusing mostly on one or a few species on a detailed level (e.g. Kellomäki *et al.* 1999; Niklas 1997; Cannell *et al.* 1988; Peltola *et al.* 2000; Brüchert *et al.* 2000). The relation between mechanical properties, crown development and plant strategies of a large number of tree species has not been studied in detail yet. This research will make a comparative study of a large number of tree species and the relation of their mechanical properties with shade-tolerance, crown development and maximum adult stature. Furthermore, mechanical properties of saplings occurring in gaps and the forest understorey will be compared.

### The mechanical design of trees

Roots, stems, branches and petioles are the supporting elements of a tree. Biomechanics put constraints on the dimensions and mechanical properties of these supporting elements. Supportive elements have to maintain their structural integrity. This means that stems and branches have to counteract the loads, exerted by for example wind, rain, own weight, without breaking. Stems or branches act like mechanical structures, such as cantilevers, *i.e.* beams or columns fixed at one end only. The sum of all loads acting on a tree must be countered by a support load exerting equally large but opposed reaction loads (Mattheck 1998). All loads, acting on a tree, flow from leaves via petioles, branches, stems and roots into the soil, supporting the tree. Structural integrity depends on internal wood characteristics (e.g. strength, modulus of elasticity, density) and exerted loads. Loads can be internal (e.g. own weight) or external (e.g. wind, rain, lianas, leaning neighbouring trees). These loads result in stresses in the supportive elements (Fig 1&2). Maintaining structural integrity means that the total stress in a cross section of a branch or stem may not exceed the maximum strength of that cross section, otherwise structural failure occurs and a stem or branch breaks. All tree species have to grow in such a way that structural integrity is guaranteed.

Species have evolved and specialised each in their own way, creating their own characteristic set of mechanical properties. Important indicators of mechanical properties are wood strength, stiffness and wood density. The wood strength ( $\text{N/mm}^2$ ) is the maximum allowable stress applied on a cross section without rupture or failure of that cross section. Under study are the bending and compression strength. Bending strength is named Modulus of Rupture (MOR). The stiffness or flexibility ( $\text{N/mm}^2$ ) is the amount of deformation or deflection in mm of a wood member under a known load in N. For flexibility Young's Modulus of Elasticity E (MOE) was used. A higher MOE indicates stiffer, less flexible wood. The wood density ( $\text{g/cm}^3$ ) is the amount of mass of wood in a unit volume (Niklas 1993a). It is strongly related to strength and stiffness. The mechanical behaviour of live tissue is being predicted. The actual loading of a stem or branch is by green wood density and maximum loading is by saturated wood density. Support costs are based on dry density, the amount of woody material invested in a branch without moisture.

There can only be one good, efficient mechanical design for a tree. Efficient means that on one hand there are no weak places with high stresses and on the other hand there are no zones with a loading stress much smaller than the maximum strength. At weak places with high stresses failure will occur first, whereas other parts of the tree easily withstand exerted loads. Zones with their maximum strength much larger than the loading stress would be useless ballast. So in an ideal tree with an optimal and efficient design every wood fibre in every cross section would have to be loaded with a stress that equals the strength. This is the axiom of uniform stress (Mattheck 1998; Niklas 1993b).

The following conditions have to be met to obtain stability for a tree as a structure with supportive members like stems and branches: **external** stability (Fig. 1). A tree is stable when the sum of all forces acting on a tree is equal to zero ( $\Sigma F_{\text{horizontal}} = 0$ ;  $\Sigma F_{\text{vertical}} = 0$ ); and the sum of all moments acting on a tree equals zero ( $\Sigma M = 0$ ). The loads on a tree, e.g. own weight, wind, rain, result in **internal** stresses (symbol  $\sigma$ ) in stem and branches (Fig. 2). The condition to be met is that

stresses in wood cross sections, due to loads, cannot exceed the maximum allowable stress, the wood strength. And as to remind, this strength varies strongly between species (Tsoumis 1991; Kollmann and Côté 1968). For example, the range of dry wood strength MOR is roughly between 55-160 N/mm<sup>2</sup> (Tsoumis 1991).

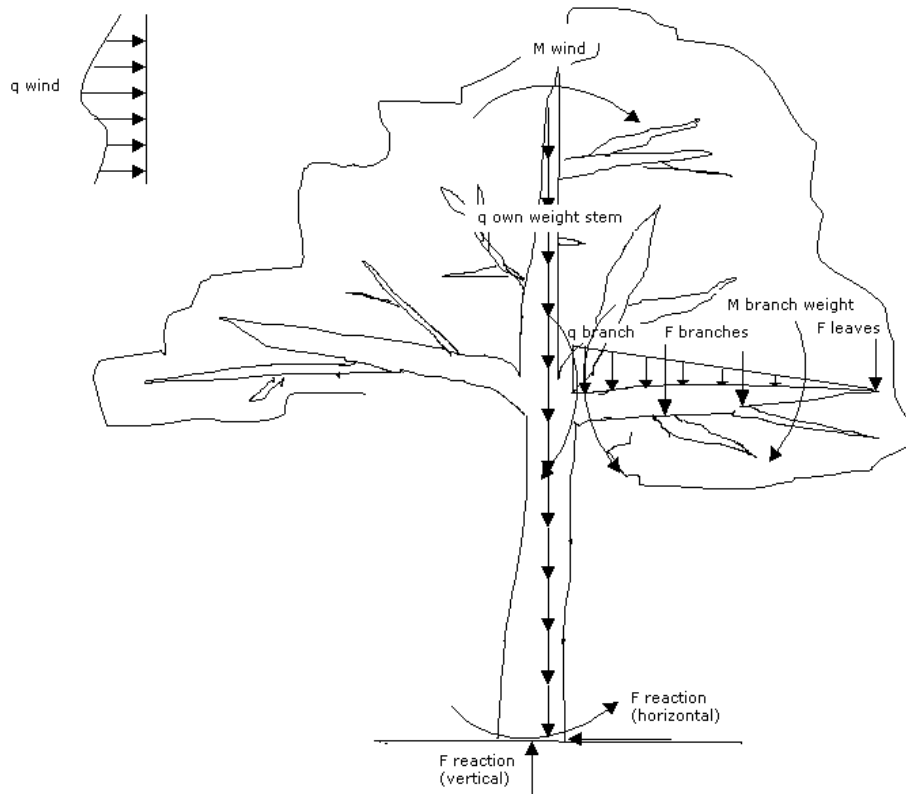


Fig. 1 **Forces:** moments (M), forces (F) acting as pointloads) and distributed loads (q) acting on trees.  $q_{wind}$  distributed wind-load;  $q_{own\ weight\ stem}$  and  $q_{own\ weight\ branch}$  along stem and branch distributed load of own weight;  $F_{leaves}$  or  $F_{branch}$  point loads caused by leaves on branch and branch on main branch or stem. **Reaction forces** in the tree:  $M_{wind}$  and  $M_{branch\ weight}$  bending moments caused by wind and branch weight; horizontal and vertical reaction load  $F_{reaction}$  and  $M_{reaction}$  anchoring the tree to solid ground.

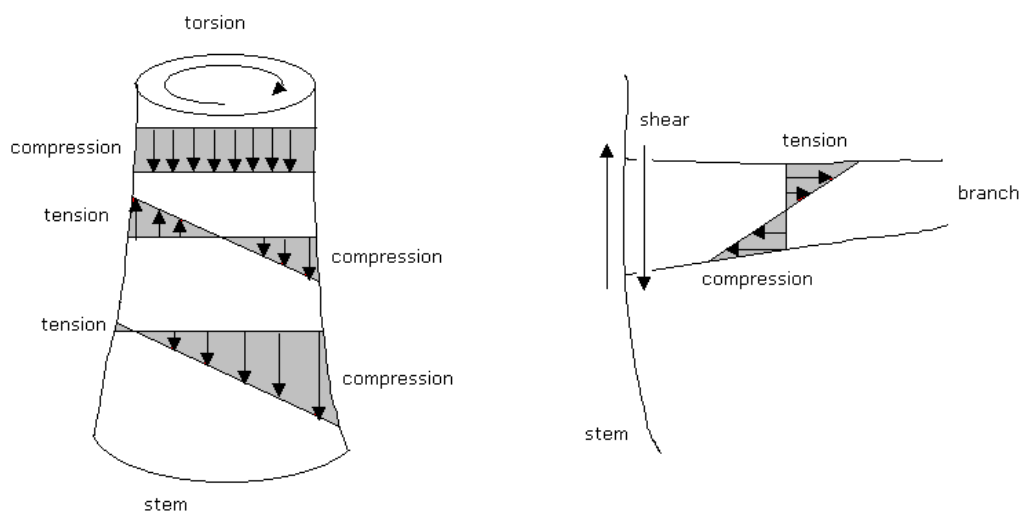


Fig. 2 **Internal stresses** in tree: compression due to axial load of own weight; tension and compression in stem and branch due to wind, eccentricity and/or branch weight; shear stress due to own weight branch (longitudinal in bending and transverse near stem); torsion due to eccentric loading by crown.

## Mechanical models

In this study two mechanical models were used. The first model consisted of tree stems carrying their own weight. According to this model trees can be regarded as upright and free-standing columns, fixed at their base (Mosbrugger 1990). In this model trees are being loaded mostly by own weight, acting as an axial compressive load (Fig. 1&2). Induced by own-weight loading tree stems show elastic instability, known as buckling. According to the Euler-Greenhill buckling formula this instability limits the maximum tree height or critical buckling length  $L_{critical}$  (Mosbrugger 1990; Sterck and Bongers 1998 and references therein).  $L_{critical}$  is related to the Modulus of Elasticity  $E$ , wood density  $\rho$  and diameter at breast height DBH:

$$L_{critical} = 0.792 (E/\rho)^{1/3} DBH^{2/3}$$

The buckling safety factor is the ratio of the critical buckling length and the observed length in the field ( $L_{critical} / L_{observed}$ ). The observed length was calculated using the formula:  $L_{observed} = H_{tree} - 130$  cm. This is the tree height above breast height, since the DBH was taken at breast height to.

The second model consisted of stems and/or branches, modelled as one side suspended beams or cantilevers, resisting a bending moment  $M$  (Mattheck 1998; Mosbrugger 1990; Morgan and Cannell 1987 & 1988). In stems bending moments usually originate from wind loads and asymmetric weight distribution of the crown. In lateral branches these bending moments originate mainly from their own weight (Fig. 3).

These bending moments result in tensile stresses in the upper half of the branch, respectively windward side of a stem and compressive stresses in the lower half, respectively leeward side. Superposition of all stresses means summing up all stresses in a cross section: with area  $A$ , axial load  $N$ , bending moment  $M$ , second order moment of area  $I$  and section modulus  $z$ , the distance between the centre of a cross section and the outermost fibre. In a circular cross section the section modulus  $z$  is equal to the radius. This results in the bending stress applied on this cross section ( $\sigma_{applied}$ ). The applied bending stress has to be smaller than or equal to the maximum allowable stress. This is the mechanical wood strength of the cross section ( $\sigma_{wood\ strength}$ ), in this case bending strength (Modulus of Rupture MOR).

$$\sigma_{applied} = N/A + (M \times z)/I \leq \sigma_{wood\ strength} \quad \text{or MOR (Verruijt, 1983)}$$

A cross section can withstand a load smaller than or equal to its strength limit, but when applied loads exceed the strength the cross section will break. This biomechanical constraint of bending results in minimum diameter requirements for stems and branches with a known angle to horizontal, length and weight. The observed own weight load  $F_{own\ weight}$  was converted into a longitudinal and perpendicular vector. The bending moment ( $M$ ) at the base of the branch is now  $F_{o.w.\ perpendicular} \times \text{arm } L$ . The longitudinal vector results in axial compression of the branch ( $N$ ) (Fig. 3). The bending safety factor is the ratio of the observed diameter and the minimum diameter ( $D_{observed} / D_{minimum}$ ).

In the mechanic model the following assumptions were made. The form of the cross-sections of stems and branches was assumed to be circular. For calculation of horizontal branch growth costs a branch was modelled as a cylindrical tube, without linear tapering. In reality tree stems and branches showed linear tapering. Linear tapering allowed uniform stress in all cross sections. Forces acting on a branch increase with decreasing distance to the stem. Every part closer to the

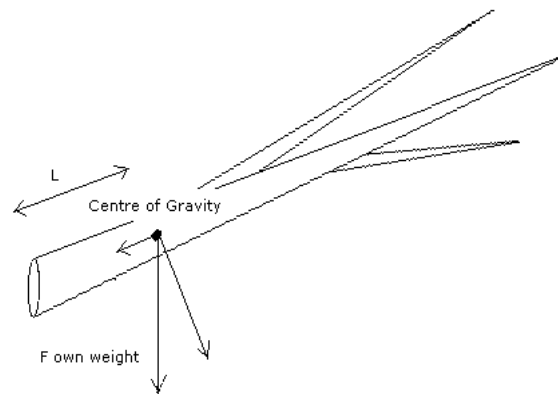


Fig. 3 Basic model of a branch, showing the position of the Centre of Gravity (CoG) and the total own weight of the branch acting in the CoG with its 2 components perpendicular and parallel to the longitudinal axis of the branch.



stem has to carry the loads of all the parts further away from the stem. By tapering the branch diameter, decreasing the diameter of the branch with increasing distance to the stem, a branch uses a minimum amount of wood with the maximum uniform stress in all cross sections of the branch, striving for economy in design (Niklas 1993b). However, the effect of linear tapering does not influence support costs to a large extent (Cannell *et al.* 1988). Besides axial compression and bending a tree has to withstand other types of stresses, for example shear and torsion stresses. Torsion loads from asymmetric crowns or the attachment of a branch to the stem (Fig. 2) can cause shear stresses. Asymmetric crowns also result in torsion stresses in the stem of a tree. However in this study design principles and calculation of branch diameters were based on bending moments and axial loads only. Furthermore, only the static loads, caused by own weight, were used and no dynamic wind or rain loads.

Based on the wood density and wood strength each species has to grow branches with minimum diameters to meet the biomechanical constraints of the second model (bending). In this case saturated density of a branch acted as the maximum load on that branch. Dry density of this branch gave the support costs of this branch. Given the interspecific differences in mechanical properties of wood and the general biomechanical constraint of bending it might be expected that there are interspecific differences in costs for growing a horizontal branch. With a different set of values for wood density and wood strength for each species the horizontal branch growth costs might differ. Ultimately this could interact with interspecific differences in crown development and adult stature.

Previous the importance of capturing the limited resource light was indicated. There are large interspecific differences in wood strength and wood density. These differences in strength and density influence biomechanical constraints with regard to buckling and bending. Interspecific differences in mechanical properties could relate to differences in horizontal branch growth costs, adult stature and shade-tolerance. Besides interspecific differences the objective is also to find differences between guilds of species, categorised on level of shade tolerance. The following research objectives and questions have been formulated. The first objective was to explore relationships among mechanical wood properties density, strength and stiffness for 30 rainforest tree species:

1. Do wood properties differ between individual saplings growing in a light versus dark environment, as found in gaps and understorey?
2. Is wood density a good predictor for wood strength? And is wood strength a good predictor for stiffness?
3. Do wood properties differ between vertical stems and horizontal branches?

The second objective was to explore if wood properties and mechanical safety factors differ between guilds, between and within species:

4. Do the different wood properties of guilds (or species) result in different buckling and bending safety factors for guilds (or species)?
5. Do vertical stems and horizontal branches have different bending safety factors, because of the different loads stems and branches experience?

The third objective was to explore the relationship between wood properties, horizontal branch growth costs, crown development and adult stature:

6. Do wood properties affect the horizontal branch growth costs?
7. Do horizontal branch growth costs affect crown development and form? Can wood properties, safety factors and horizontal branch growth costs be related to the maximum adult stature?

## Methodology

### Site and species

This research was conducted within the 100,000 ha forestry concession La Chonta, located in the province of Guarayos (15°47'S, 62°55'W) in the department of Santa Cruz, Bolivia. The forest represents a transition zone between dry forest types and the Amazonian forests. The site was classified as a Subtropical Humid Forest according to the Holdridge system (Bolfor, Studyplan and references therein). The forest soils are low fertility soils, i.e. oxisols, inceptisols and ultisols. The mean annual precipitation is 1,560 mm with a dry season lasting from May until October. The mean annual temperature is 25.3° Celsius (La Chonta 1998). The forest cover is seasonal with about 1/3 of the canopy species losing their leaves during the dry season. Over 150 tree species grow at La Chonta. About 18 species are being considered commercially valuable, but only 8-10 species are currently being harvested in significant quantities in cutting cycles of 30 years. The area is part of a large scale long-term silvicultural research project of the Instituto Boliviano de Investigacion Forestal (IBIF). Within the area treatment plots of roughly 27 ha with permanent transects were established. For the plots there are 3 silvicultural treatments (normal, improved and intensive management) and a "semi"-control group (liana cuttings on some harvestable trees).

In total 30 tree species, belonging to 21 families were selected for this study (BOLFOR 2003; IBIF and BOLFOR 2004). The species had a large range in wood density, thus also a large range in wood strength (MOR: 7.6 up to 87.6 N/mm<sup>2</sup>; Appendix: summary table). Furthermore species were selected based on their shade-tolerance. Four guilds were distinguished based on Finegan (1992): shade tolerant species (ST) that can establish and survive in the shade; partial shade tolerant species (PST) that can establish in the shade, but need a gap to grow to larger sizes; long-lived pioneers (LLP) that have high light requirements for regeneration and live longer than 30 years; short-lived pioneers (P) that have high light requirements for successful regeneration and live up to 30 years. The 30 species were classified according to Poorter *et al.* (in press): 11 shade-tolerant, 9 partial shade-tolerant, 6 long-lived pioneer and 4 pioneer species.

### Design and measurements

For all species under study 5 individuals in light and 5 individuals in dark growing conditions were selected, resulting in 300 individuals. Individuals were selected based on a stratified random design. The strata were dark and light growth conditions for saplings. For describing the growth conditions of saplings the crown position was estimated by 2 independent observers. The adjusted Dawkins' Crown Position Index (CPI) scale after Clark and Clark (1992) with 7 classes was used: 1 = no direct light; 1.5 = low amount of lateral light; 2 = medium amount of lateral light; 2.5 = high amount of lateral light; 3 = partial overhead light; 4 = >90% of the crown area receives direct overhead light; 5 = emergent crown with direct light from all directions (Clark and Clark 1992; Dawkins and Field, 1978). Individuals with a CPI < 2.5 undergo dark growth conditions and individuals with a CPI ≥ 2.5 light growth conditions (Sterck *et al.* 1998). A random selection of individuals within each stratum was made. The ontogenetic stage of all individuals was the same to minimise ontogenetic variation. Height ranged from 1.75 up to 4 m with an average of 2.89 m. The diameter at breast height (DBH) ranged from 5.9 to 36.5 mm with an average of 17.8 mm.

Individuals were measured for their morphology and mechanical design. For morphology these variables were measured: the diameter at breast height (DBH), the height of the tree, the height of the lowest branch, the height of the crown and the diameter of the crown. The DBH was measured with marking gauge (±0.05 mm); the height of the tree, of the crown and of the lowest branch and the crown width were measured with a semi-flexible measuring tape (±0.5 cm). For the mechanical design several characteristics of branches were measured. From each individual the most horizontally and the terminal metre of the most vertically oriented branch or stem-part were selected. The following properties of these branches and stems were measured: the length of the branch from base to tip, the diameter at the base of the branch, the weight, the angle with regard to the horizontal of the first 50 cm starting from the base of the branch and the position of the Centre of Gravity (CoG) of the branch. The CoG or mass centre is a point where the resultant of the gravitational forces pulls on the branch. First the branch was separated from the tree. Then the

CoG was determined by balancing the branch on a pencil. The position of the pencil where the branch stayed stable in horizontal position was regarded as the working line of the CoG (Fig. 3). The length of the branch and the position of the CoG were measured with a semi-flexible measuring tape ( $\pm 0.5$  cm); diameters were measured with a marking gauge ( $\pm 0.05$  mm); weight by a spring balance ( $\pm 0.5$  g); angles with a simple levelling instrument combined with a so called "wave hook" and a protractor (arch with degrees) to determine degrees ( $\pm 0.5^\circ$ ).

From both horizontal and vertical branches 2 sub-samples were taken with a length/diameter ratio of at least 18 to determine wood properties. From these sub-samples the following properties were determined: green volume, saturated, green and dry weight. Green volume was calculated using the length ( $\pm 0.5$  mm) and diameters ( $\pm 0.05$  mm) at begin and end of the sample, using formulas based on cone volumes. Weights were measured with a balance ( $\pm 0.05$  g). Green weight was measured on the day of collection. One subset of the samples was submerged under water for 4 to 5 days before measuring the saturated weight. The other subset was put in an oven to dry for 4 days at  $70^\circ$  Celsius. Important notice is that for all samples that whenever wood density or wood strength and stiffness is mentioned, it was measured on a specimen with bark. All densities were calculated using the green volume.

For measuring wood strength and stiffness from each individual tree 2 stem-parts with a diameter of about 20 mm were collected. From these sub-samples the green volume and the green and saturated weight were determined. Furthermore the Modulus of Rupture (MOR), the compression strength (CS) and the stiffness or Young's Modulus of Elasticity (MOE) were measured on saturated specimen, resulting in the lowest strength values. Dry wood is stronger than saturated wood (Kollmann and Côté 1968). The specimen requirements of the wood samples were: length/height ratio of the test sample was  $\geq 18$  and the sample's average span/height ratio is 16; this should be larger than 15 to minimise disturbing effects on the measured MOR (Kollmann and Côté 1968).

For each sample the MOR was determined using a loading equipment, applying loads ( $\pm 1.25$  kg) with a certain speed on a sample (Fig. 4A). The speed of testing MOR for each sample was roughly 3 minutes, with a deflection speed varying between 1.5 and 3 mm/s. The load with accompanied deflection was recorded for each load interval of 2.5 kg, resulting in load-deflection diagrams (Fig. 4B). From this recorded relation between applied load and deflection with the Deflection formula (Fig. 4A) MOE or E in static bending was calculated. MOE was based on the first, linear, elastic part of the load deflection diagram (fig 4B). A steeper line indicates a higher value for MOE, thus a stiffer wood

For compression tests specimens with a height of 5 cm were prepared. The same loading equipment was used, but now the load was applied axially on the specimen until the maximum load was reached. At this point the cross sections failed, indicating that the applied stress equalled the maximum allowable stress in compression, the CS. The speed of testing was on average 1 minute per specimen. Only the maximum load was recorded.

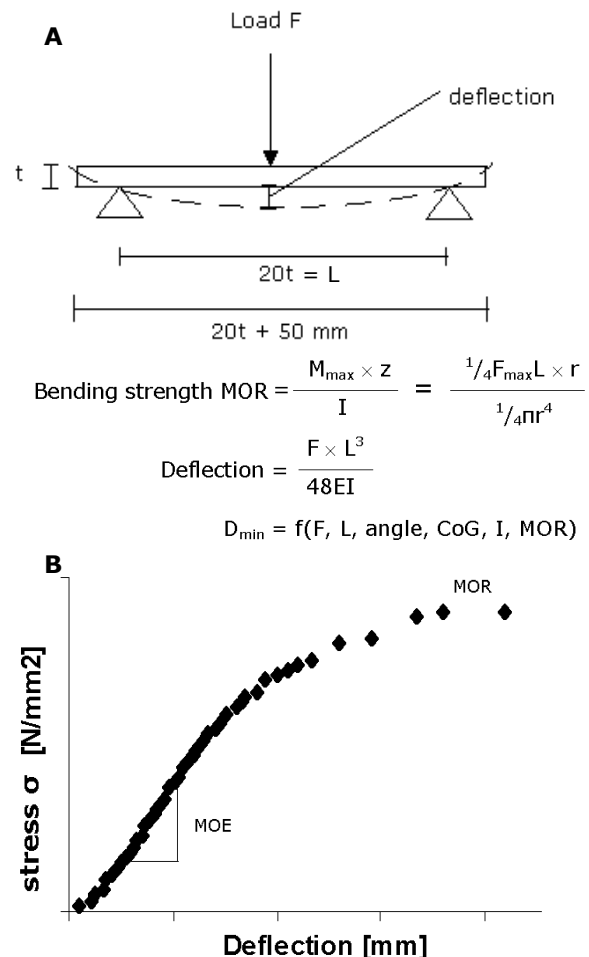


Fig. 4 (A) Static bending test on sample with length L, t is height of sample, for circular cross section  $t=D=2r$ , with formulas for MOR and Deflection; (B) typical load-deflection diagram indicating MOR as maximum allowable stress and MOE as function of steepness of first part of load deflection diagram

To evaluate the wood strength only compression and bending strength were measured. Torsion, tensile and shear strength require special, difficult to prepare samples and special equipment. Therefore these strengths could not be measured within this research. If needed, MOR could be used as a rough indicator for tensile strength (Tsoumis 1991).

### Data analysis

The first objective was to explore the relationship between the mechanical wood properties of the 30 species. The first research question was about wood properties of dark-grown versus light-grown individuals ( $CPI < 2.5$  versus  $CPI \geq 2.5$ ). These differences between dark- and light-grown individuals were tested with Mann-Whitney U tests (no normality) and t-tests (normality), with  $n=300$ . Differences in light response between species were tested ( $n=300$ ) with a 2-way ANOVA, dependent variable density, strength or stiffness and with independent variables species and light class (2 light classes  $CPI <$  or  $\geq 2.5$ ). Differences in light response between guilds were tested ( $n=30$ ) with another 2-way ANOVA with dependent variable density, strength or stiffness and with independent variables guilds and light class. By using species averages pseudo-replication was avoided. For the second research question the relations between the mechanical properties of wood were tested with linear regressions for MOR, CS and MOE as dependent variables with dry, green and saturated density respectively as independent variables or predictors. Since no differences in light response were detected (see results) regressions were based on pooled averages per species ( $n=30$ ). Thirdly, group differences in density between horizontal branches and vertical stems were analysed with Wilcoxon signed ranks tests. Horizontal and vertical samples came from the same individual tree, so were regarded as matched samples.

The second objective was to explore if wood properties and mechanical safety factors differ between guilds, between and within species. Effects of biomechanical constraints were tested for buckling and bending criteria, using safety factors in plant design to analyse the fourth research question. The buckling safety factor is the ratio of the critical buckling length and the observed length in the field ( $L_{critical} / L_{observed}$ ). Correlation analyses were used to identify relations between the critical buckling length and the observed length in the field, based on individuals ( $n=300$ ) and on species averages ( $n=30$ ). Differences in safety factor between guilds were tested with a 1-way ANOVA. The bending safety factor is the ratio of the observed diameter and the minimum diameter ( $D_{observed} / D_{minimum}$ ). Relations between observed and minimum diameter were tested using correlation tests for both individuals and species averages. For the fifth part of the analyses correlations were performed separately for horizontal branches and vertical stems. Given the different loads acting horizontal and vertical parts there might be differences expected between the two.

The third objective was to explore the relationship between wood properties, horizontal branch growth costs, crown development and adult stature. To answer question six, horizontal branch growth costs were calculated per species using saturated density as maximum load and dry density as growth costs. Minimum diameter requirements were calculated for 1 m length of a branch based on the bending criterion. The specific set of wood density and wood strength for each species might lead to different horizontal growth costs. Growth costs differences between guilds were tested with Kruskal Wallis. Instead of using guilds as an ordinal scale a second analysis was made using a continuous interval scale of the juvenile crown exposure index at 5 m of height (CE5). CE5 is the observed, average crown exposure of individuals with 5 m height in the study area (Poorter *et al.* in press). CE5 was based on the Crown Position Index by Dawkins and Field (1978). This gave each species a unique value of CE5, indicating the level of light demand or shade tolerance. The seventh and final question analysed the effect of horizontal branch growth costs on crown development and maximum adult stature. The maximum adult stature was obtained from Poorter *et al.* (in press). The effect of growth costs on crown development was tested using linear regression with horizontal branch growth costs as a predictor for the proportion of horizontal branches in the crown, crown diameter, crown height and crown slenderness. Crown slenderness is the crown height divided by the crown diameter. The relation between maximum adult stature and wood density and strength were tested with correlation analyses. Similar correlation analyses were executed for maximum adult stature and the derived variables buckling and bending safety factors and horizontal branch growth costs.

## Results

First the effect of light and dark growth conditions on wood properties was given. Then the linear regression analyses for wood properties were presented, followed by differences in wood properties between horizontal branches and vertical stems. Next step was the tests regarding the biomechanical constraints on buckling and bending safety factors. Last results were regarding horizontal branch growth costs, crown development and maximum adult stature.

### Effect of light conditions on wood properties

The data showed no significant differences in wood properties for light- (CPI $\geq$ 2.5) versus dark-grown (CPI $<$ 2.5) individuals. Various tests were performed, but no significant difference was found between dark and light individuals for wood properties such as density and strength (Table 1).

Table 1 Median values for density and strength for dark- vs. light-grown individuals: significance of differences densities and strengths; green, saturated and dry density for horizontal branches and vertical stem-parts; bending strength Modulus of Rupture, compression strength and Modulus of Elasticity; a Mann-Whitney U test, 2 independent samples was carried out.

Wood properties	Median		Test-statistic			
	dark	light	U (or t)	P	n	
Density (g/cm <sup>3</sup> )						
Green	horizontal	0.99	0.98	9556	ns	284
	vertical	1.00	1.03	10436	ns	300
Saturated	horizontal	1.02	1.04	<sup>t</sup> 0.11	ns	284
	vertical	1.04	1.05	10803	ns	300
Dry	horizontal	0.44	0.43	9665	ns	284
	vertical	0.41	0.41	10972	ns	300
Strength (N/mm <sup>2</sup> )						
Modulus of Rupture	50.6	52.3	<sup>t</sup> 0.37	ns	300	
Compression strength	18.9	19.1	10707	ns	300	
Modulus of Elasticity	5012	4601	<sup>t</sup> 1.56	ns	300	

<sup>t</sup> t-value - normally distributed independent samples t-test; ns P $>$ 0.05

With a 2-way ANOVA was established that density and strength differed significantly between species. Light class and the interaction species-light class had no significant effect on the wood properties (Table 2). Only for MOE light class had a significant effect, but here the interaction had a significant effect also.

Table 2 Values of test-statistic F and significance level for species, light class and interaction. A two-way ANOVA was carried out with wood property = f(**species**, light class); 30 species with 2 light classes were used. Average wood properties per species were presented in the appendix: summary table species. The 2 light classes were dark-grown (Crown Position Index CPI  $<$  2.5) and light-grown individuals (CPI $>$ 2.5).

Wood properties	Test-statistic F			n	
	Species	Light class	Interaction		
Density (g/cm <sup>3</sup> )					
Green	horizontal	21.23 ***	1.97 ns	0.76 ns	284
	vertical	24.81 ***	2.10 ns	1.31 ns	300
Saturated	horizontal	10.97 ***	0.01 ns	0.99 ns	284
	vertical	33.48 ***	3.29 ns	1.47 ns	300
Dry	horizontal	41.90 ***	2.82 ns	0.71 ns	284
	vertical	49.00 ***	2.15 ns	1.36 ns	300
Strength (N/mm <sup>2</sup> )					
Modulus of Rupture	46.68 ***	0.75 ns	1.30 ns	300	
Compression strength	42.01 ***	2.08 ns	1.30 ns	300	
Modulus of Elasticity	19.41 ***	6.96 **	1.70 *	300	

ns P $>$ 0.05; \* P $\leq$ 0.05; \*\* P $\leq$ 0.01; \*\*\* P $\leq$ 0.001

With a 2-way ANOVA was established that density and strength decreased along the successional gradient from shade-tolerant to pioneer guild. Light class and the interaction guild-light class had no significant effect on the wood properties (Table 3).

Table 3 Average wood properties per guild. For all guilds together and for each guild separately the average value of the wood properties was given per light class. A two-way ANOVA was carried out: wood property =  $f(\text{guilds}, \text{light class})$ . 4 guilds and 2 light classes were used: dark-grown (Crown Position Index CPI < 2.5) and light-grown individuals (CPI>2.5).

Wood properties	Averages per Guild										P-value ANOVA				
	All guilds n=30		Shade-tolerant n=11		Partial shade-tolerant n=9		Long-lived pioneer n=6		Pioneer n=4		guild	Light class	Inter- action	n	
			dark	light	dark	light	dark	light	dark	light					dark
Density (g/cm <sup>3</sup> )															
Green	horizontal	0.96	0.95	1.03	1.01	1.00	0.99	0.91	0.92	0.78	0.75	***	ns	ns	29
	vertical	0.98	1.00	1.09	1.09	1.00	1.01	0.91	0.96	0.76	0.77	***	ns	ns	30
Saturated	horizontal	1.01	1.01	1.08	1.08	1.05	1.04	0.95	0.96	0.83	0.80	***	ns	ns	29
	vertical	1.03	1.05	1.15	1.14	1.06	1.07	0.92	1.02	0.80	0.81	***	ns	ns	30
Dry	horizontal	0.41	0.39	0.48	0.47	0.44	0.43	0.36	0.34	0.19	0.19	***	ns	ns	29
	vertical	0.40	0.39	0.49	0.47	0.42	0.41	0.34	0.32	0.17	0.19	***	ns	ns	30
Strength (N/mm <sup>2</sup> )															
Modulus of Rupture		50.6	49.7	60.4	60.7	55.1	51.8	46.0	46.7	20.6	19.5	***	ns	ns	30
Compression strength		18.8	18.3	22.1	21.3	21.0	20.0	17.1	17.1	7.6	7.6	***	ns	ns	30
Modulus of Elasticity		5137	4769	5657	5102	5142	4904	5446	4873	3226	3392	*	ns	ns	30

ns P>0.05; \* P≤0.05; \*\* P≤0.01; \*\*\* P≤0.001

Furthermore the buckling safety factor of dark-grown versus light-grown individuals did not differ significantly (Mann-Whitney U Z=-0.800 P=0.424). There was no clear pattern to discover, or a group of species, disturbing a general pattern for differences within species for dark- vs. light-grown individuals. Finally, analyses showed that the bending safety factor did not differ significantly between dark- and light-grown individuals (independent samples Mann-Whitney U test: horizontal branches Z=-0.158 P=0.874; vertical branches Z=-0.512 P=0.608).

Since no dark-light effects could be detected in the data, it was appropriate to pool the 5 dark individuals with the 5 light individuals per species. So, for each species analyses were made based on a total of 10 individuals.

## Mechanical properties of wood

The wood density was a good predictor of the mechanical properties of the species. The Modulus of Rupture (MOR), the Compression Strength (CS) and the Modulus of Elasticity (MOE) increased with density (Table 4; Fig. 5). The strongest predictor of mechanical properties was the dry wood density. The second strongest predictor was the saturated density, leaving green density as last in line. Furthermore the explaining power of the linear regression model was the strongest for MOR, followed by CS and MOE.

Two species, *Jacaratia spinosa*, a long-lived pioneer, and *Urera sp.*, a pioneer species, were relative outliers (Fig. 5 encircled markers). These species showed a moderate green and saturated density with a very low value of MOR, CS and MOE. The wood of both species can absorb a relatively large amount of water, having the largest differences in green and saturated density vs. dry density. Both had relatively weak wood, compared to the other species.

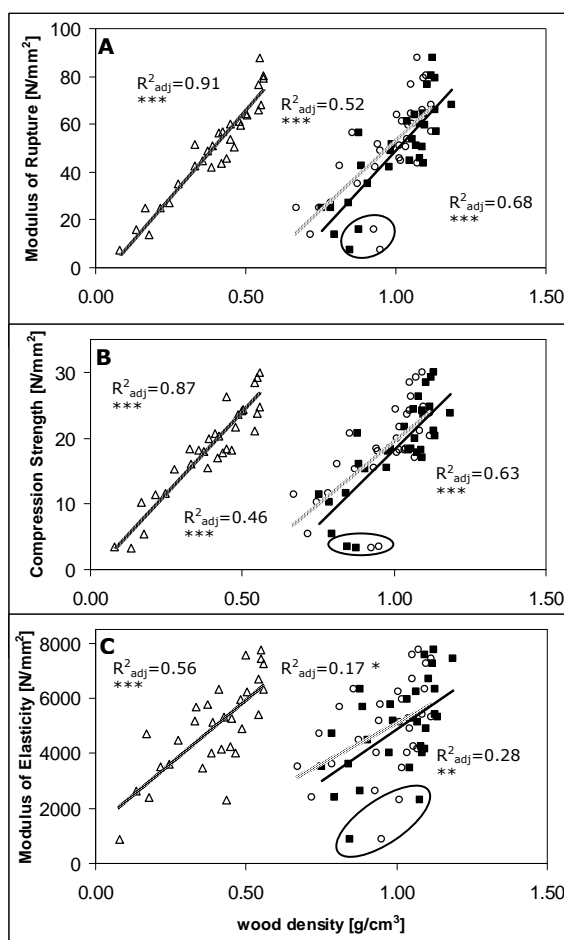


Fig. 5 Regression analyses with dry ( $\Delta$ ), green (O) and saturated (!) density as predictors for A: Modulus of Rupture, B: Compression strength and C: Modulus of Elasticity. For each regression line the level of determination  $R^2_{adj}$  and the level of significance were given (\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ ). Encircled were *Jacaratia spinosa* and *Urera sp.* as relative outliers.

Table 4 Regression coefficients for Modulus of Rupture (MOR), Compression Strength (CS) and Modulus of Elasticity (MOE) based on 30 rain forest tree species. Independent variables are wood densities (green, saturated and dry). Regression coefficients related to the equation  $y = a + bx$ , e.g.  $MOR = -5.0 + 140 * (\text{dry density})$ . The significance level P and coefficient of determination  $R^2_{adj}$  were given (see also Fig. 5).

		Regression coefficients			
y	Wood Density (x)	b	a	$R^2_{adj}$	P
MOR	Dry	140.69	-5.03	0.91	***
	Green	119.42	-65.89	0.52	***
	Saturated	135.85	-86.83	0.68	***
CS	Dry	47.71	-0.19	0.87	***
	Green	38.84	-19.21	0.46	***
	Saturated	45.53	-27.38	0.63	***
MOE	Dry	9326	1293	0.56	***
	Green	5988	-876	0.17	*
	Saturated	7523	-2334	0.28	**

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$

There was a tight relationship between the Modulus of Rupture and the Modulus of Elasticity. With increasing MOR, the MOE increased as well (Fig. 6). In other words: stronger wood tended to be less flexible ( $MOE = 1397 + 70.88 * MOR$ ;  $n=30$ ;  $P<0.001$ ). *Jacaratia spinosa* turned out to be a relative outlier again. This species had the lowest MOR and MOE, thus its wood was weakest and most flexible. *Erythrochiton fallax* was a species that deviated also a little from the strong general trend. The wood of *Erythrochiton fallax* was relatively flexible ( $MOE = 2302 \text{ N/mm}^2$ ) given its bending strength ( $MOR = 46 \text{ N/mm}^2$ ) (Fig. 6 encircled markers).

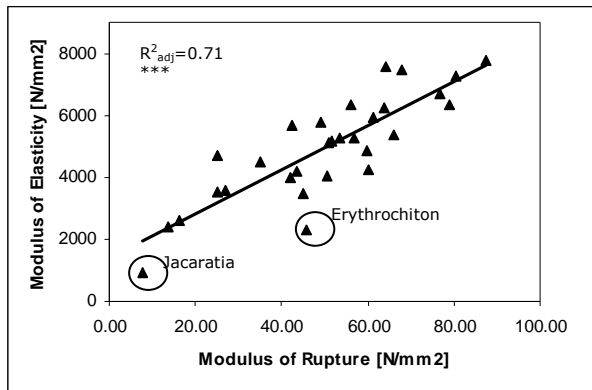


Fig. 6 Relationship between Modulus of Elasticity (MOE) and Modulus of Rupture (MOR), with the regression line (level of determination  $R^2_{adj}$  and level of significance \*\*\*  $P \leq 0.001$ ). Encircled are *Jacaratia spinosa* and *Erythrochiton fallax* as relative outliers.

### Density of vertical stems and horizontal branches

For each sapling the difference in density of the horizontal branch and vertical stem was compared using a matched sample test. Striking was that green and saturated density of horizontal parts were lower than that of vertical parts. For the dry density the effect was the opposite; horizontal parts had higher densities than vertical parts (Fig. 7 & 8).

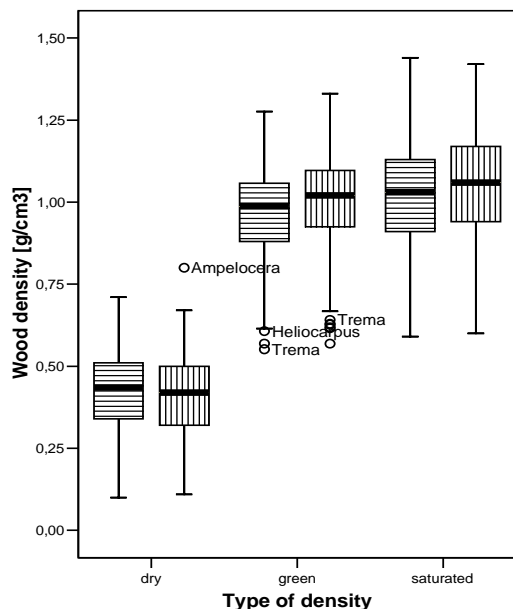


Fig. 7 Wood density boxplots for horizontal branches (horizontally marked boxes) and vertical stems (vertically marked boxes) for the 3 types of density on the horizontal axis (dry, green and saturated). The horizontal density differed significantly from the vertical (Wilcoxon signed ranks test,  $n=284$ ; dry density:  $Z=-2.720$ ,  $P=0.007$ ; green density:  $Z=-5.549$ ,  $P<0.001$ ; saturated density:  $Z=-3.351$ ,  $P=0.001$ ).



Green and saturated density showed a lower horizontal than vertical wood density, especially for the shade-tolerant guild (Fig. 8). When all 4 guilds were pooled together the horizontal density differed from vertical density (Fig. 7 & Table 5). This general trend could not be established in case of the guilds being tested separately. Especially for pioneer species horizontal density did not differ from vertical density (Table 5).

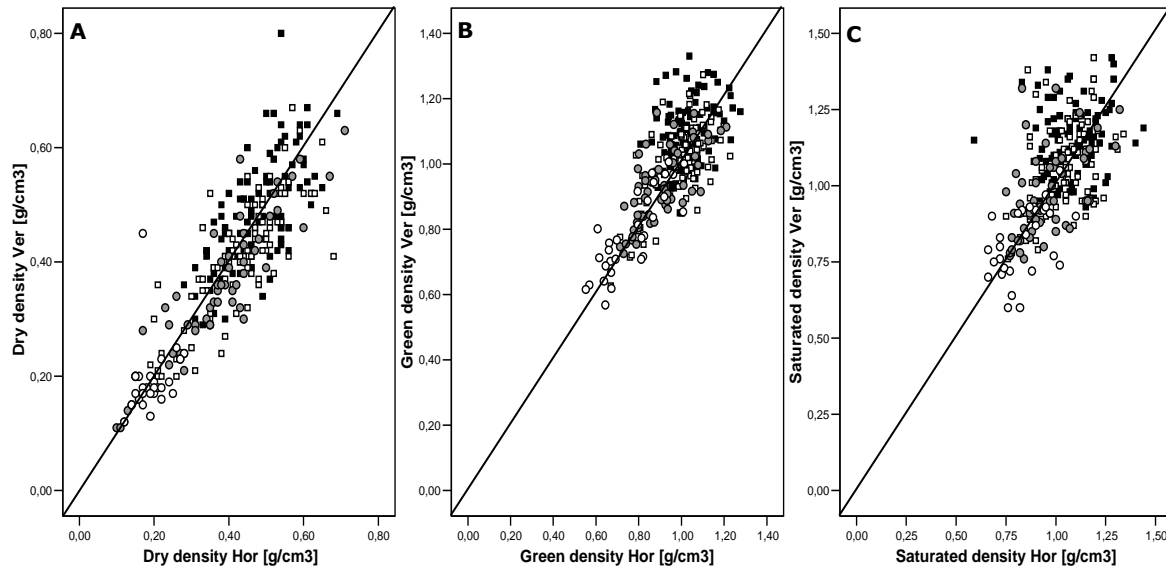


Figure 8: Scatterplots of vertical against horizontal density for dry (A), green (B) and saturated (C) density. Each point represents an individual tree ( $n=284$ ) and for each point the guild to which the individual tree belongs was given: ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer. In each scatterplot a line was drawn for the equation Vertical density = Horizontal density.

Table 5 Median density values of horizontal branches and vertical stem-parts; Median density was calculated for dry, green and saturated wood, for all guilds pooled together and for each guild separately; A matched samples Wilcoxon signed ranks test was carried out to test group differences between horizontal and vertical density.

Median density ( $\text{g}/\text{cm}^3$ )	n	Dry density			Green density			Saturated density		
		horizontal	vertical	P	horizontal	vertical	P	horizontal	vertical	P
All guilds	284	0.44	0.42	**	0.99	1.02	***	1.03	1.06	***
Shade-tolerant	110	0.47	0.47	ns	1.01	1.08	***	1.07	1.14	***
Partial shade-tolerant	90	0.45	0.41	***	1.01	1.02	ns	1.05	1.06	ns
Long-lived pioneer	54	0.38	0.35	**	0.89	0.92	ns	0.93	0.95	ns
Pioneer	30	0.19	0.18	ns	0.80	0.77	ns	0.84	0.84	ns

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$

The wood properties differed a lot between species. On average the density and strength decreased along the succesional gradient from shade-tolerant to pioneer (Fig. 9). However, within the guilds a lot of variation in wood properties existed. A more recognisable difference in density can be seen for the averaged values for the 4 guilds (Fig. 10).

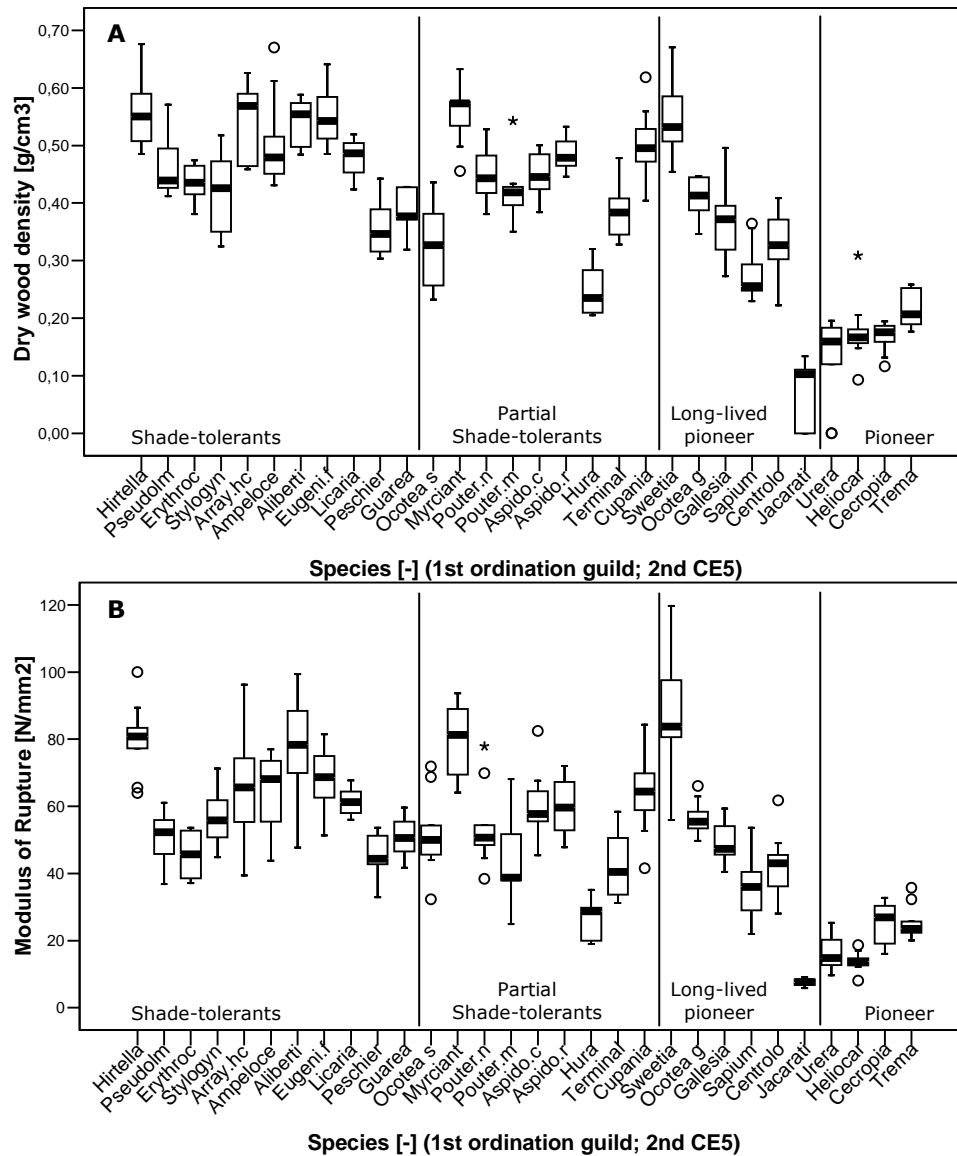


Fig. 9 Boxplots showing dry wood density (A) and Modulus of Rupture MOR (B) for the set of 30 species. Horizontal axis species were ordinated based on guild order from left to right: shade-tolerant; partial shade-tolerant; long-lived pioneer; pioneer. Within guilds the species were ordered with increasing average juvenile crown exposure (CE5) from left to right. Vertical axis gives dry density in g/cm<sup>3</sup> (A) and MOR in N/mm<sup>2</sup> (B).

Per guild the differences in densities were tested previously with a 2-way ANOVA with guild and light (dark- vs. light-grown individuals) as independent variables (Table 3). Since no differences in light response were detected, light class was excluded from the analyses, pooling the dark- and light-grown individuals together. Therefore, a 1-way ANOVA was executed with density only depending on guild. For the dry, green and saturated density for both horizontal and vertical branches density differed very highly significantly between guilds. For all cases the density decreases going from shade-tolerant, partial shade-tolerant, long-lived pioneer to pioneer (Fig. 10).

Based on the 2-way ANOVA analyses (Table 3) MOR and CS differed significantly between guilds. MOE did differ significantly between guilds, but here the light class and the interaction lightclass-guild were significant (Table 3). Next, a 1-way ANOVA with only guilds as independent variable was performed. MOR and CS decreased along the successional gradient from shade-tolerant to pioneer. MOE did not differ significantly between guilds (MOR  $F=6.37$   $P=0.002$ ; CS  $F=7.08$   $P=0.001$ ;  $F=1.65$   $P=0.20$ ).

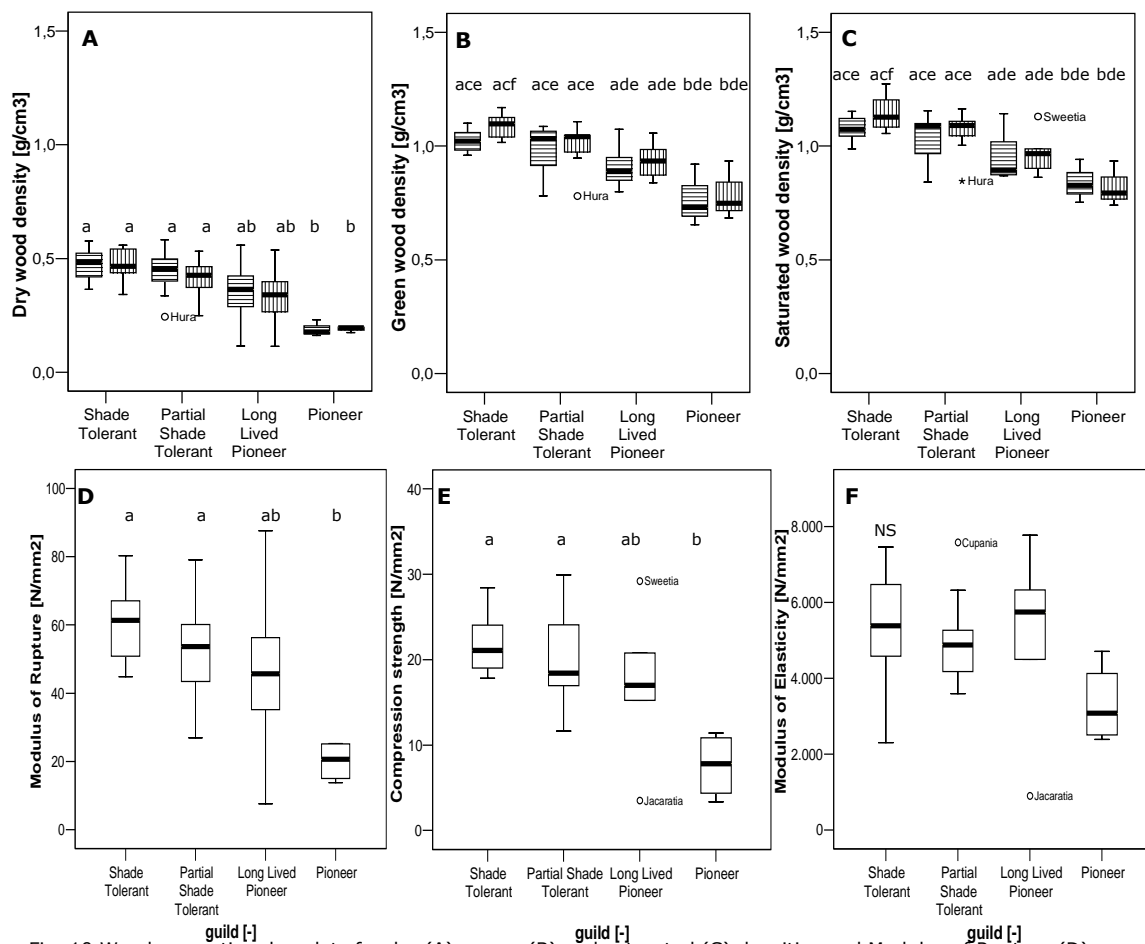


Fig. 10 Wood properties: boxplots for dry (A), green (B) and saturated (C) densities and Modulus of Rupture (D), Compression Strength (E) and Modulus of Elasticity (F). Wood properties were given per guild (shade-tolerant; partial shade-tolerant; long-lived pioneer; pioneer). In panels A, B and C the horizontally marked boxes represent densities of horizontal branches; the vertically marked boxes represent vertical stems. In panels D, E and F the wood strength was not known for horizontal and vertical separately. Significant wood properties differences between guilds were indicated with a, b etc. with NS meaning non-significant (PostHoc Tukey test).

## Biomechanical constraints: Testing diameters based on buckling criterion and bending criterion

### Buckling criterion

The buckling safety factor was the ratio of observed length and critical buckling length. The buckling safety factor increased with density. There was almost a significant correlation between the buckling safety factor and green or saturated density of vertical parts. But for the dry density there was a significant correlation with the buckling safety factor. The critical buckling length was plotted versus the observed length (Fig. 11A & C) and the buckling safety factor against saturated density of vertical parts (Fig. 11B & D). The saturated density was used, since the critical buckling length was calculated with the maximum load caused by saturated density. Again species *Jacaratia spinosa* deviated from the other species, having the lowest buckling safety factor (Fig. 11C & D).

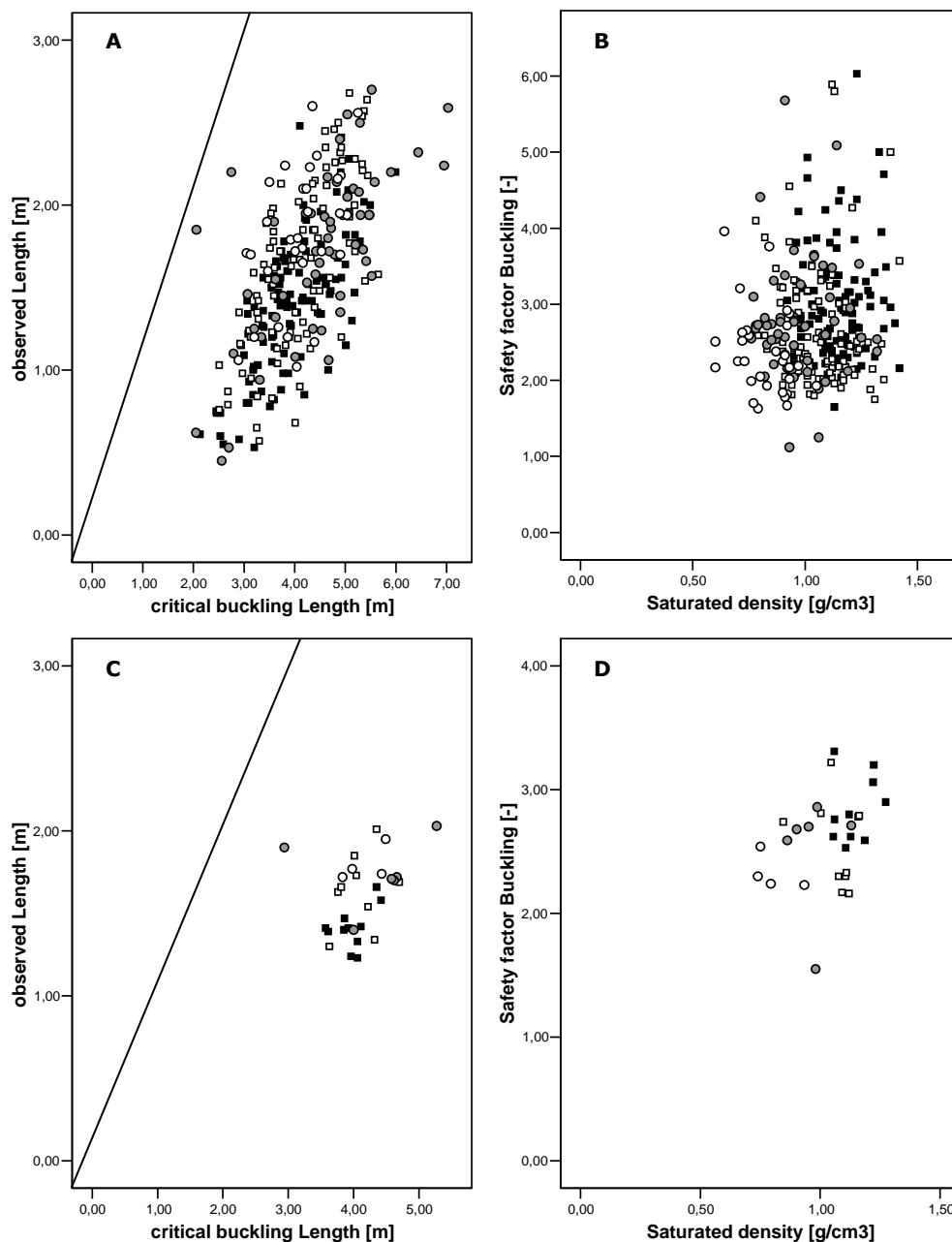


Fig. 11 Observed Length plotted against Critical buckling Length for all individuals (A) and for species averages (C). Safety factor buckling against saturated density for all individuals (B) and for species averages (D). Symbols represent: ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; O pioneer. In A and C a line was drawn for observed length = critical buckling length. Spearman Rho,  $n=300$ , Safety Factor-saturated density: correlation coefficient  $r=0.110$   $P=0.056$ ; Safety Factor-green density:  $r=0.104$   $P=0.073$  and Safety Factor-dry density  $r=0.162$   $P=0.005$ .

The buckling safety factor differed significantly between the 30 species (Kruskal-Wallis test: Chi-square=87.2 df=29  $P<0.001$ ). However, the buckling safety factor differed almost significantly between the 4 guilds, using species as unit of replication (1-way ANOVA,  $n=30$   $F=2.84$   $P=0.057$ ). The trend was that the buckling safety factor decreased along the successional gradient going from shade-tolerant to pioneer species.

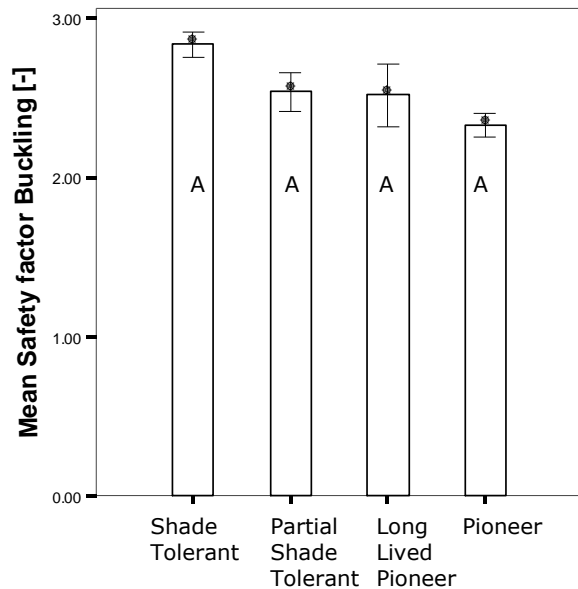


Fig. 12 Mean buckling safety factor per guild (shade-tolerant, partial shade-tolerant, long-lived pioneer and pioneer). Error bars indicate Standard error of mean. The buckling safety factor almost differed significantly between guilds, indicated by letter A (1-way ANOVA,  $n=30$   $F=2.84$   $P=0.057$ ).

### Bending criterion

With the weight, the Centre of Gravity, the mechanical properties and the wood density the minimum diameters for each tested branch were calculated, based on the bending formula. First thing tested was the relation between observed and predicted diameter of branches and stems (Fig. 13). The relation observed and predicted diameter was stronger for horizontal branches (Fig. 13A; Spearman  $\rho=0.85$   $P<0.001$ ) than for vertical stems (Fig. 13B; Spearman  $\rho=0.42$   $P<0.001$ ). Based on average diameters per species there was a positive correlation between minimum and observed diameter of horizontal branches (Fig. 13C; Spearman  $\rho=0.65$   $P<0.001$ ). Also for minimum and observed diameter of vertical stems there was a positive correlation (Fig. 13D; Spearman  $\rho=0.43$   $P=0.02$ ).

Predicted branch diameters, based on the mechanical model, were always smaller than observed branch diameters, except one case. For vertical branches more scatter was observed, and predicted diameters deviated more from observed diameters, compared with horizontal branches. The values of the bending safety factor ( $D_{\text{observed}} / D_{\text{minimum}}$ ) were larger for the vertical stems (Fig. 13 & 14). According to the individuals data ( $n=284$ ) the bending safety factor differed significantly between horizontal and vertical branches (Wilcoxon, matched pairs,  $Z=-13.865$ ,  $P<0.001$ ).

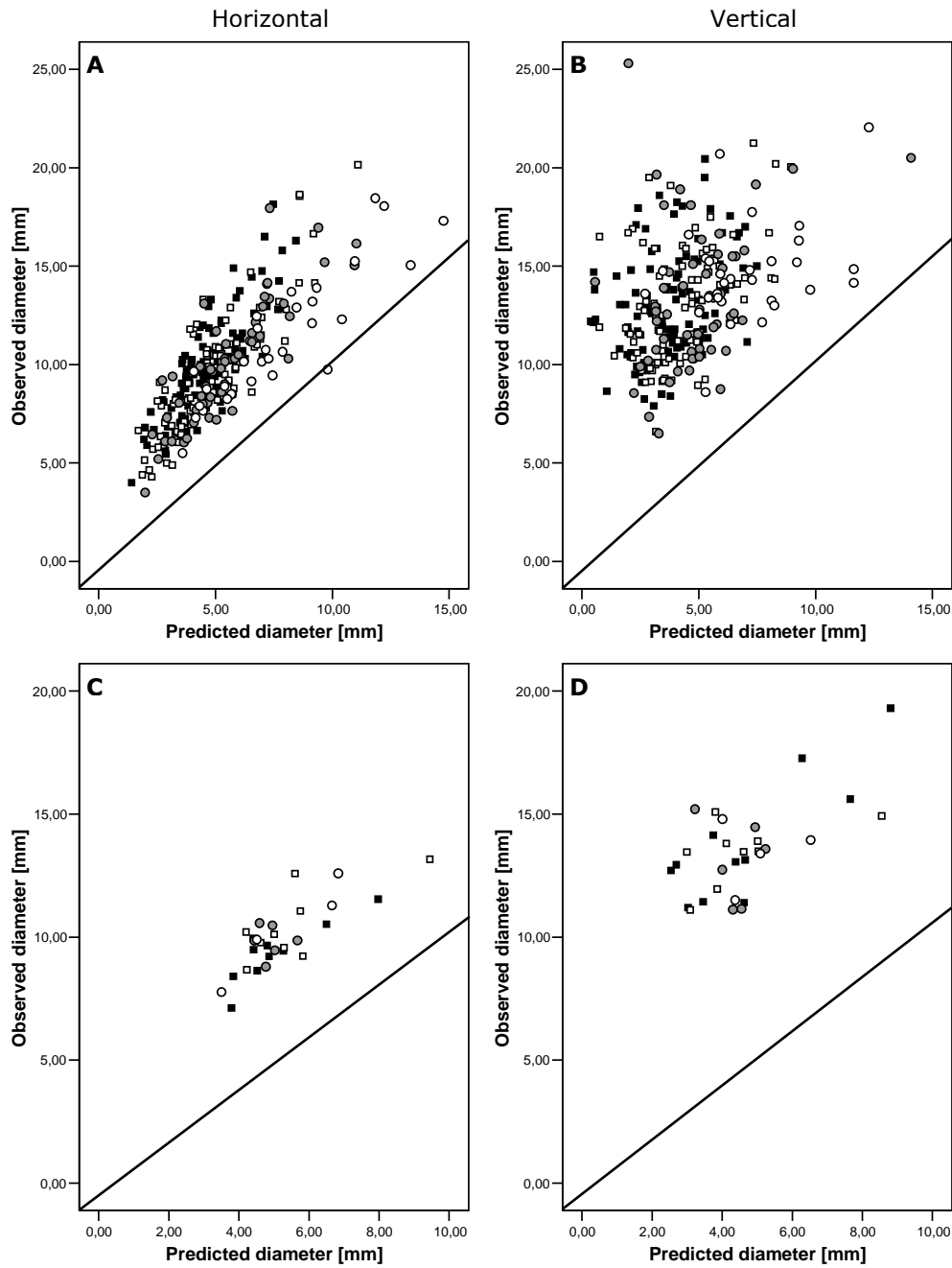


Fig. 13 Observed diameter versus predicted diameter based on bending criterion for horizontal branches and vertical stems; panels A & B represent all individuals; panels C & D species averages; A & C horizontal branches and B & D vertical stems. The line in the figures represents  $D_{observed} = D_{minimum}$ . Symbols represent the guilds: ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer.

The bending safety factor did not differ significantly between guilds (Fig. 14; 1-way ANOVA  $n=30$ ; Horizontal branches  $F=0.68$   $P=0.57$ ; Vertical stems  $F=0.33$   $P=0.81$ ). Analysed on species level can be concluded that between species there is a significant difference in bending safety factor for both horizontal and vertical parts ( $n=284$ ; Kruskal Wallis test; horizontal Chi-square = 106.459,  $df = 28$   $P<0.001$ ; vertical Chi-square = 122.602,  $df = 29$   $P<0.001$ ).

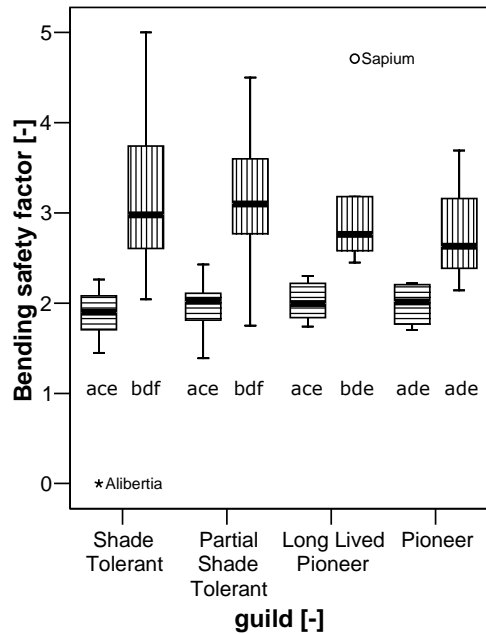


Fig. 14 Bending safety factor boxplots ( $D_{\text{observed}}/D_{\text{minimum}}$ ) for the guilds shade-tolerant, partial shade-tolerant, long-lived pioneer and pioneer. Horizontally marked boxes represent horizontal branches, vertically marked boxes vertical stems. Bending safety factor did not differ significantly between guilds (1-way ANOVA  $n=30$ ; Horizontal branches  $F=0.68$   $P=0.57$ ; Vertical stems  $F=0.33$   $P=0.81$ ), but horizontal and vertical bending safety factor differed (Posthoc Tukey test, homogeneous subgroups indicated by a, b etc.)

## Horizontal branch growth costs

The dry weight needed to grow a horizontal branch of 1 m was calculated, based on minimum diameter requirements for horizontal branches in pure bending. The load of the branch depended on the saturated wood density, and the growth costs on the dry density. There was a strong positive correlation between dry and saturated density (Fig. 15).

The data was not normally distributed; therefore a Kruskal Wallis test was executed. Horizontal branch growth costs did not differ significantly between the 4 guilds (Fig. 16). The outlier in the guild long-lived pioneer was caused by *Jacaratia spinosa*, an extremely bad performer in horizontal branch growth. However, even with leaving *Jacaratia spinosa* out of the analysis, branch growth costs did not differ significantly between guilds. Furthermore, huge variation existed within the pioneer guild.

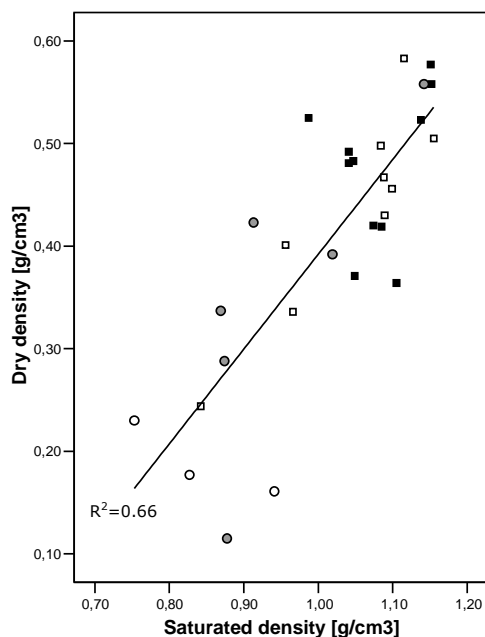


Fig. 15 Correlation horizontal branch growth costs (i.e. dry density) vs. maximum load (i.e. saturated density) Correlation  $n=29$  Spearman's  $\rho=0.78$   $P<0.001$ . Symbols represent the guilds ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer

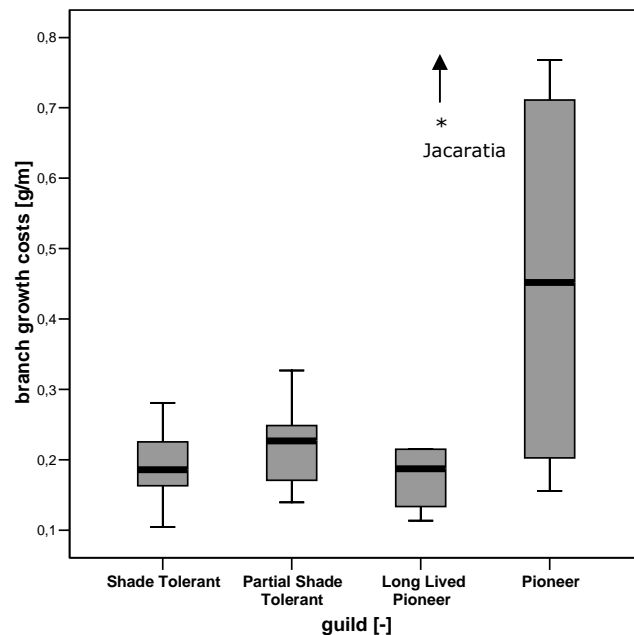


Fig. 16 Boxplots horizontal branch growth costs per m branch for guilds (Kruskal Wallis  $n=30$ ; chi-square=3.29 df=3  $P=0.349$ ). Species *Jacaratia spinosa* was an extreme outlier with 1.85 g/m branch growth costs.



Instead of testing branch growth costs differences between guilds, a Spearman Rho correlation was carried out for the horizontal branch growth efficiency and the average juvenile crown exposure index at 5 m height (CE5). There was a significant, positive correlation ( $P=0.05$ ); horizontal branch growth costs increased with increase of CE5 the (Fig. 17). Long lived pioneer *Jacaratia spinosa* deviated from the rest, having the highest branch growth costs. Furthermore, the 4 pioneer species deviated a lot within the pioneer group. Two pioneers, *Cecropia concolor* and *Trema micrantha* were located below the correlation line, indicating relatively low branch growth costs. Whereas pioneers *Urera sp.* and *Heliocarpus americanus* were situated above the line, indicating relatively high costs.

Branch growth costs did not correlate significantly with juvenile crown exposure, when leaving *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus* out of the test. The Spearman correlation coefficient also decreased. No significant correlation was found when all pioneers and *Jacaratia spinosa* were excluded.

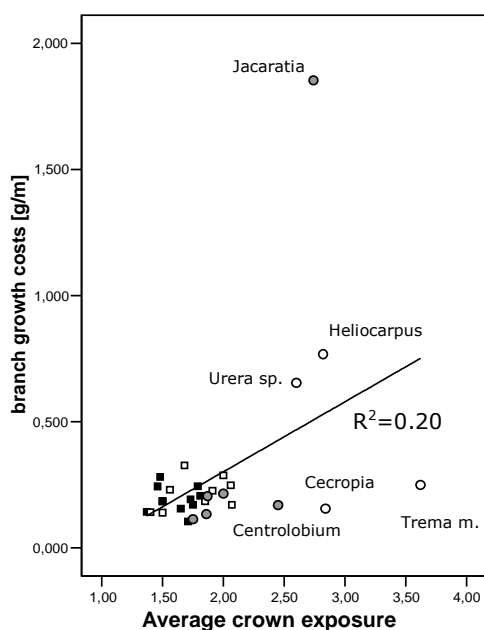


Figure 17 Correlation Horizontal branch growth costs vs. average Juvenile Crown Exposure at 5m tree height. ( $n=30$  Spearman's  $\rho=0.36$   $P=0.05$ ). *Jacaratia spinosa* was the outlier with the highest growth costs. Symbols represent the guilds ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer.

### Horizontal growth investment versus crown development and maximum adult stature

On a more general level trends in life history traits and their relation with mechanical characteristics were explored. Differences between species and guilds in density and strength were significant, it is interesting whether these differences can explain certain trends in life history traits, such as maximum adult stature, crown width, crown slenderness ( $H_{\text{crown}} / D_{\text{crown}}$ ) and related to this the proportion of horizontal branches.

The proportion of horizontal branches decreased significantly when horizontal branch growth costs increased (Fig. 18A). However, *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus* deviated extremely from the rest. Excluding these 3 species resulted in a non-significant relationship between proportion and costs (Fig. 18B).

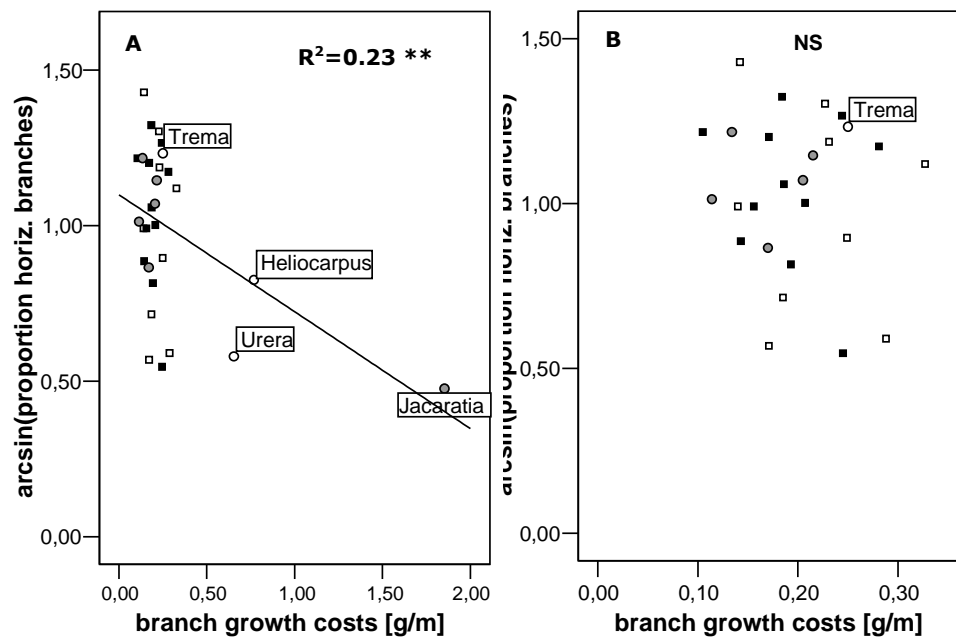


Fig. 18 Regression proportion of horizontal branches vs. horizontal branch growth costs; (A) all species; significant regression  $\arcsin(\text{propHbranch})=1.10-0.38(\text{Hbranch growth costs})$   $P=0.009$ ; (B) *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus a.* excluded; non significant  $\arcsin(\text{propHbranch})=1.12-0.45(\text{Hbranch growth costs})$   $P=0.615$ . Symbols represent the guilds ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer.

Furthermore, species developed less wide crowns with high horizontal growth costs (Fig. 19A). Excluding *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus*, which deviated again, still resulted in species developing less wide crowns with high horizontal growth costs (Fig. 19B). There was no significant relation with Crown height (P=0.062) nor Crown slenderness (P=0.937).

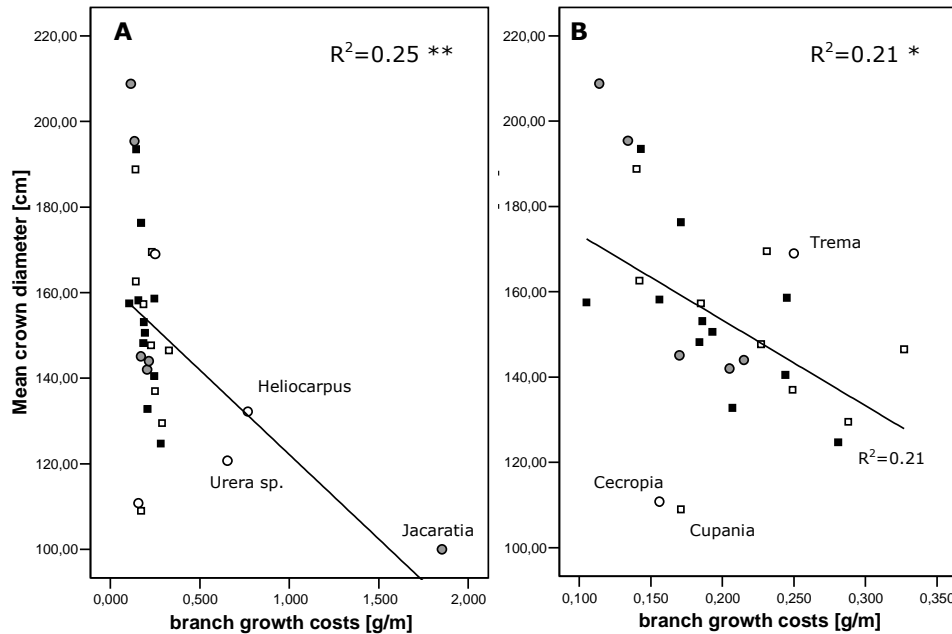


Figure 19 Regression Mean crown diameter vs. horizontal branch growth costs  
 (A) all species, significant: crown diameter=161-39(horizontal branch growth costs) \*\* P=0.005;  
 (B) *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus a.* excluded, significant: crown diameter=194-201(horizontal branch growth costs) \* P=0.017 Symbols represent the guilds ! shade tolerant; □ partial shade tolerant; ● long-lived pioneer; ○ pioneer.

Maximum adult stature involves criteria like: buckling height (based on wood properties MOE and saturated density); bending and compression criteria (based on MOR, CS and saturated density); horizontal growth costs (MOR, saturated and dry density). Maximum adult stature did not correlate significantly with any of the wood properties, neither safety factors, nor growth costs (Table 6 & Fig. 20). The trend seemed that wood density, strength and safety factor decreased with an increase in maximum adult stature. The horizontal branch growth costs seemed to increase with an increase in maximum adult stature.

Table 6 Correlation coefficients for maximum adult stature related to wood density and strength, buckling and bending safety factors and horizontal growth costs. Normally distributed variables were tested with Pearson correlation, not-normally distributed variables with Spearman (n=30)

Maximum adult stature			Pearson Correlation	p-value
	units			
Saturated wood density Vertical	g/cm <sup>3</sup>		-0.352	0.056
Modulus of Rupture	N/mm <sup>2</sup>		-0.188	0.319
Compression strength	N/mm <sup>2</sup>		-0.103	0.589
Modulus of Elasticity	N/mm <sup>2</sup>		-0.087	0.649
Buckling safety factor	-		-0.244	0.194
Bending safety factor Vertical	-		-0.229	0.222
		Spearman's rho		
Dry wood density Vertical	g/cm <sup>3</sup>		-0.279	0.136
Horizontal branch growth costs	g/m		0.116	0.540

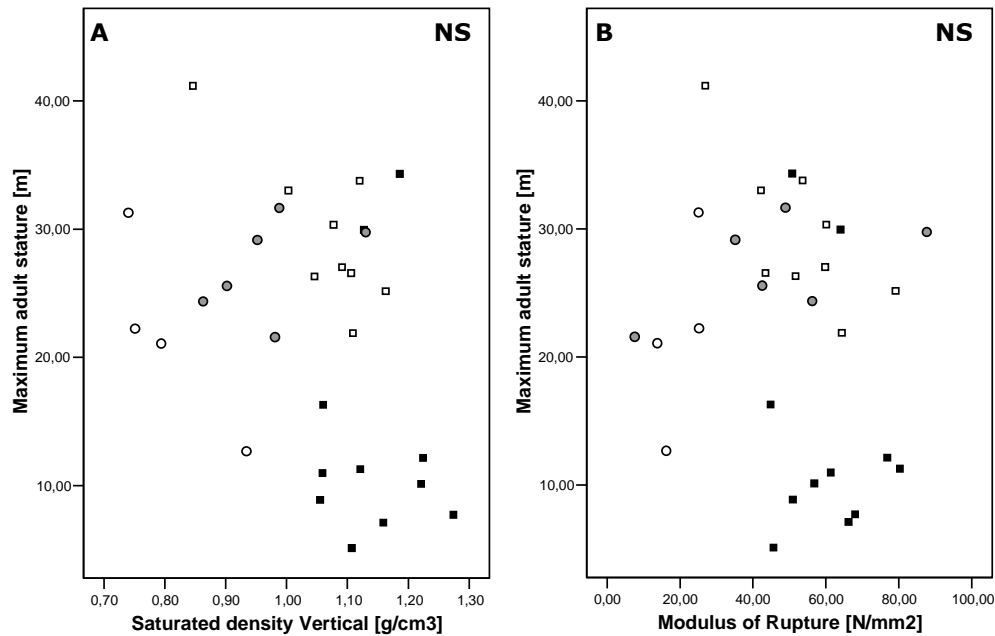


Figure 20 Scatterplots Maximum adult stature against (A) saturated density and (B) Modulus of Rupture. Both graphs did not show any significant correlation (NS;  $n=30$  Pearson correlation, Table 6). Symbols represent the guilds:  $\blacksquare$  shade tolerant;  $\square$  partial shade tolerant;  $\bullet$  long-lived pioneer;  $\circ$  pioneer.

The set of 30 species was divided into 2 groups: a shade-group consisting of shade-tolerant and partial shade-tolerant species and a pioneer group of long-lived pioneer and pioneer species. Striking result was that opposed correlations were found the 2 groups.

For the shade group the trend seemed that wood density, strength and safety factor decreased with an increase in maximum adult stature. The pioneer group showed the opposite: wood density, strength and safety factor increased with an increase in maximum adult stature.

For the shade group the horizontal branch growth costs increased with an increase in maximum adult stature. For the pioneer group the growth costs decreased with an increase in maximum adult stature (Table 7 & Fig. 21). Only the bending safety factor deviated, but no significant correlation with adult stature was found.

Table 7 Correlation coefficients for maximum adult stature related to wood density and strength, buckling and bending safety factors and horizontal growth costs. Species were assigned to the shade group (partial- and shade tolerant) or the pioneer group (long lived- and pioneer). Normally distributed variables were tested with Pearson correlation, not-normally distributed variables with Spearman.

Maximum adult stature		Shade group (n=20)		Pioneer group (n=10)	
	units	Pearson Correlation	P-value	Pearson Correlation	P-value
Saturated wood density Vertical	$\text{g/cm}^3$	-0.497	<b>0.026</b>	0.164	0.650
Dry wood density Vertical	$\text{g/cm}^3$	-0.486	<b>0.030</b>	0.523	0.121
Modulus of Rupture	$\text{N/mm}^2$	-0.425	0.062	0.556	0.095
Compression strength	$\text{N/mm}^2$	-0.305	0.192	0.677	<b>0.031</b>
Modulus of Elasticity	$\text{N/mm}^2$	-0.267	0.255	0.552	0.098
Buckling safety factor	-	-0.405	0.076	0.520	0.123
Bending safety factor Vertical	-	-0.277	0.238	0.757	<b>0.011</b>
		Spearman's rho		Spearman's rho	
Horizontal branch growth costs	$\text{g/m}$	0.245	0.297	-0.455	0.187

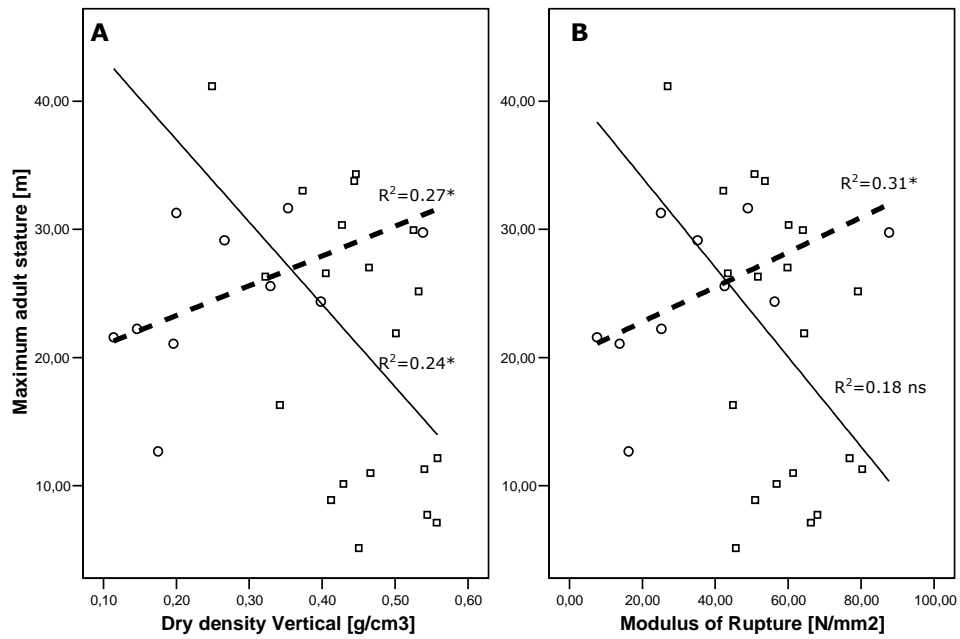


Fig. 21 Scatterplots Maximum adult stature against (A) dry density and (B) Modulus of Rupture. Symbols represent □ shade group and O pioneer group. Dashed lines represent pioneer group and solid lines represent shade-group. Shade- and pioneer group showed opposite correlations for maximum adult stature vs. density and stature vs. strength; ns non significant; \* P < 0.05 (table 7).

## Discussion

### Mechanical wood properties density, strength and stiffness for 30 rainforest tree species

#### 1. Do wood properties differ between light or dark-grown individual saplings?

In this study no differences were detected in density and strength of light- and dark-grown individuals as found in gaps and understorey. Tests were performed on individuals, species and guilds level and none resulted in a significant light response (Table 1-3). In general in high light all species tend to grow faster in height. Height growth rates of light demanding species were higher than that of shade-tolerant species (King 1994; Poorter & Bongers in press). In medium shade *Quercus petraea* seedlings had the largest rates of increase in wood thickness and produced more fibres, compared to extreme light and shade conditions (Igboanugo 1990). Wood density, crown size and light environment are major determinants of tree growth. Within species, growth rate increased linearly with light interception. Observed interspecific differences in growth rate (mm/year) were linked to interspecific differences in wood density and light interception (King *et al.* 2005).

Despite results of earlier research (*e.g.* King *et al.* 2005), in this study no differences in light response were detected. The Crown Position Index (CPI) of dark-grown individuals was significantly lower than the CPI of light-grown individuals, both within guilds and for all species pooled. The average CPI of the shade-tolerant group was not significant lower than that of the pioneer group. Perhaps sampling only saplings of relative young age caused more similarity in density and strength. Wood density increased with age (Niklas 1997). So for older trees differences could become larger, whilst for younger trees no significant differences appeared.

Since there were no significant dark-light differences in this data set, for all the other analyses the 5 dark individuals and the 5 light individuals were pooled together for each species. Averages of all variables were based on 10 individuals per species.

#### 2. Is wood density a good predictor for wood strength? And is wood strength a good predictor for stiffness?

For the given set of species wood density was a very good predictor of wood strength. Modulus of Rupture (MOR), compression strength (CS) and wood stiffness (MOE) increased with increasing density (Fig. 5; Table 4). This result was in line with earlier findings (Niklas 1993a; Tsoumis 1991; Kollmann and Côté 1968). Based on linear regression dry, green and saturated density were significantly capable of predicting MOR, compression strength and MOE. Dry density is the strongest predictor, for example a  $R^2_{adj}$  of 0.91, followed by saturated and last green density.

Wood strength mainly originates from woody fibres (Kollmann and Côté 1968). This might be the explanation why dry density was the strongest predictor, since dry wood consists mainly of fibres. Saturating wood counteracted temporal differences in green density. Collecting wood samples on different times could cause some samples to be collected after heavy rainfall and other samples after a period of relative drought. This could explain why green density was the weakest predictor, showing more variation.

For the 3 mechanical wood properties density explained MOR best ( $R^2_{adj}$  up to 0.91), followed by CS ( $R^2_{adj}$  up to 0.87) and last MOE ( $R^2_{adj}$  up to 0.56). The relative low level of determination for MOE could be related to the methods used. The available loading equipment had a scale with scale units of 2.5 kg for weight increment. For MOR and CS this seemed accurate enough. MOE was calculated from the first linear part of the load-deflection diagrams. In this first part loads were still relatively low, compared to the maximum strengths MOR. Therefore, the scale unit of 2.5 kg was less accurate for measuring and calculating MOE. Finally for this set of species the stiffness of wood MOE increases with increasing wood strength MOR (Fig. 6). This means that in general stronger wood is stiffer, less flexible. This was comparable with earlier findings (Niklas 1993a).

### 3. Do wood properties differ between vertical stems and horizontal branches?

Dry, green and saturated wood density differed highly significantly between vertical stems and horizontal branches, analysis based on all species. For dry density the horizontal density was higher than the vertical density. The opposite was presented for green and saturated density: the horizontal density was lower than the vertical density (Fig. 7 & 8). Dry, green and saturated wood density did not differ significantly between vertical stems and horizontal branches, when the analysis was executed per successional guild, but the trend seemed the same. For dry density the horizontal density was higher than the vertical density. For green and saturated density the horizontal density was lower than the vertical density (Fig. 10; Table 5).

Given the static load schemes on horizontal and vertical parts it was expected that horizontal branches need to grow stronger wood than vertical stems. But on the other hand besides mechanics and loads other functions are of influence. For example a stem is more important for survival of the whole plant than a branch. From this perspective investing in stronger wood and/or more mechanical safety for the stem would be appropriate.

Horizontal branches undergo larger static bending loads than vertical stems. In all cases the minimum required diameter for bending loads far exceeded the minimum diameter for compression loads. For horizontal branches the minimum required diameter for bending was on average a factor 27 higher than for compression, given the weight and angle of the branch (Fig. 3). For vertical stems the average factor was 9. With the positive linear relation between strength and density it was expected that horizontal density was higher than the vertical density. This only was correct for the dry density. For green and saturated density the horizontal density is lower than the vertical density. An explanation could be that vertical stems have a relatively higher importance for the transportation of water and nutrients than the horizontal branches. There are differences in conductivity; vertical stems have a higher conductivity than horizontal branches (Wilson, 2000). Therefore stems have relatively more or larger vessels than in branches. This gives stems the ability to absorb or carry more water, thus a higher green and saturated density, while relatively less fibres are present, giving a lower dry density, compared to horizontal branches.

Testing wood strength for horizontal and vertical wood samples would give extra information on strength differences between horizontal and vertical parts. The samples tested for strength were from a lower part of the stem and not from the terminal metre of the stem. In this research only strength of this lower, vertical part could be tested, so only horizontal versus vertical density differences could be analysed.

### **Differences in wood properties and mechanical safety factors between guilds, between and within species**

#### 4. Are differences in wood properties between species and guilds responsible for differences in buckling and bending safety factors?

It was expected that faster growing pioneer species grow wood with less density than slow growing shade-tolerant species. Between the 30 species density and strength differed significantly (Fig. 9). Dividing the 30 species in the 4 shade-tolerance guilds resulted in very highly significant differences in densities between the 4 guilds. Density decreased along the successional gradient going from shade-tolerant, partial shade-tolerant, long-lived pioneer to pioneer. Also MOR and CS decreased along the successional gradient. MOE showed the same trend, but without significance (Fig. 10).

Species with lower wood density have lower construction costs, and consequently growth rates are inversely correlated with wood density among tropical tree species. Higher wood density is thought to confer a survival advantage, reducing the probability of physical damage and possibly fungal infection (Muller-Landau and references therein 2004). Observed interspecific differences in diameter growth rate (mm/year) were linked to interspecific differences in wood density and light interception (King *et al.* 2005). Height growth rates of light demanding species were higher than that of shade-tolerant species (King 1994). Relative growth rates (diameter increase in cm/years)

decreased with wood density (Chamber et al, 2004). The same was found by Muller-Landau (2004) for saplings and trees and by King et al (2005) for pole-sized trees. Wood density was found to be significantly negatively correlated with light establishment preference (Slik 2005).

#### Buckling safety factor

It was expected that pioneer species would have a lower buckling safety factor, due to their rapid height growth and consequently low construction costs needed. There were significant differences in the buckling safety factor between species, but not between guilds. The trend seemed that the buckling safety factor decreased from shade-tolerant, partial shade-tolerant, long-lived pioneer to pioneer species (Fig. 11 & 12).

According to King (1994) height growth rates of light demanding species are higher than those of shade-tolerant species. Poorter et al (2003) found that light demanding species need a slender stem, (thus a lower safety factor), to attain or maintain a position in the canopy. Species with a lower wood density have lower construction costs (Muller-Landau and references therein, 2004). To maintain low construction costs a lower buckling safety factor would be appropriate for fast-growing pioneers. For shade-tolerant species having a higher buckling safety factor could relate to a survival advantage, reducing the probability of physical damage by falling debris. Shade-tolerant species spend more time in the understorey, this increases the risk of damage by falling debris, compared to pioneer species.

The buckling safety factors averaged per species ranged from 1.5 up to 3.5 with the majority of species around 2.5. This indicated that the saplings had a safe margin and either no economic design in terms of wood invested in the stem, not all loads were accounted, or the formula for critical buckling length gave an overestimation. According to Niklas and Spatz (2004) growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. The relation between diameter and plant height was violated, leading to an overestimation of plant height based on buckling safety (Niklas and Spatz 2004). The formula for critical buckling length did not directly incorporate dynamic loads as wind, rain or falling debris. The buckling safety factors will decrease, when these dynamic loads would be taken into account and added to the static own weight loads. Furthermore, 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 supporting their own weight.

Nevertheless, the Euler-Greenhill buckling formula was suitable for a comparative analysis of interspecific differences in buckling safety factors. In this comparative analysis all species showed an overestimation of critical buckling length, related to observed length. But differences in buckling safety factors between species and between guilds were more important than the absolute value of buckling safety factors. Comparing small saplings on the forest floor means that all saplings undergo more or less the same loads. Wind loads will be relative small, but rain and falling debris could be of higher importance. Incorporating wind loads together with static loads into the buckling formula would decrease buckling safety factors, but interspecific differences will remain and would be expected to be the same as without wind loads.

#### Bending safety factor

It was expected that pioneer species, again due to their rapid growth, would have lower bending safety factors than shade-tolerant species. The bending safety factor differed significantly between species, for both horizontal and vertical parts. However, the bending safety factor did not differ significantly between guilds and did not show a trend (Fig. 13 & 14).

Plausible explanation could be that due to different branching patterns pioneers were able to maintain the same bending safety factor as shade tolerants. Architectural groups, defined in terms of developmental rules differed in branch shape and angle (King, 1998). A more upward orientation and less or closer to the base of the main branch positioned lateral branches minimise bending loads and therefore, support costs (Morgan and Cannell, 1988).



On one hand it could be expected that bending safety factors of horizontal branches would be lower than those of vertical stems, given the static loads of their own weight. But on the other hand why would vertical stems not adapt to their static loads, and grow more slender with a lower bending safety factor. Nevertheless, analyses showed that bending safety factors are lower for horizontal branches, compared to vertical stems.

In the case of bending safety factors adding wind loads to the static loads would decrease the bending safety factor of vertical stems more than that of horizontal branches. Adding wind loads would increase the bending stresses in stems relatively stronger, compared to branches. Consequently, adding wind load to stems would result in relative more increase of bending stresses, compared with horizontal branches. Adding wind loads to stems increases results in far more bending stresses in stems, than that are occurring now due to their static own weight load and their angle to the horizontal. Bending stresses were more important for mechanical design of stems and branches than compression stresses. It seems that wind loads have a larger effect on the mechanical design of stems than of horizontal branches. In the case of comparing bending safety factors of horizontal and vertical branches I have to agree with Niklas (2000), that using only static loads would be insufficient, but still suitable for interspecific comparisons.

The maximum values of bending safety factors were caused by stems with a 90 degree angle to the horizontal; these branches did not undergo static bending stresses. In all calculated cases the minimum diameter based on bending was larger than the minimum diameter based on compression. Compression alone did not play an important role in minimum diameter based on static stresses. Even in vertical parts with maximum compression the relative small bending stresses still resulted in larger minimum diameters than compression stresses did.

### **The influence of wood properties on horizontal branch growth costs and crown development**

#### 5. Do wood properties affect the horizontal branch growth costs?

Based on dry density as growth costs and the saturated density as maximum load it might be expected that species and guilds differ in horizontal branch growth costs. And indeed horizontal branch growth costs differed significantly between species.

For pioneers a low ratio dry and saturated density could mean low growth costs (dry density) per load (saturated density). But an important third variable in this comparison is the MOR. Pioneers in this study had a very low MOR, compared to shade-tolerants. Now, for guilds one would expect the following: despite the low ratio dry and saturated density for pioneers, a very low MOR results in higher horizontal branch growth costs for pioneers, related to shade-tolerants. The low value of MOR could implicate thicker branches needed to prevent breaking by bending. However, this could not be accepted, horizontal branch growth costs had no significant difference between guilds (Fig. 16). This could be related to the point already made for the bending safety factor. Bending loads can be minimised by a more upward orientation of the branches, less lateral branches or lateral branches positioned closer to the base of the main branch. Consequently support costs will be minimised too (Morgan and Cannell 1988).

The categorical scale of guilds was changed into a continuous scale of average crown exposure. This made a correlation analysis possible. Pioneers had a higher average juvenile crown exposure than shade-tolerants. It was expected that species with a higher average crown exposure would have higher horizontal branch growth costs. This was confirmed by the analysis, as there was a significant, positive correlation ( $P=0.05$ ) between horizontal extension costs and crown exposure (Fig. 17). The horizontal extension costs increased with an increase of crown exposure. Species with a higher average crown exposure or pioneers invest more in height than lateral extension. Investing energy in height growth rather than lateral crown growth allows a rapid vertical stem extension, but the crown diameter has to be sufficiently small to reduce the risk of mechanical failure (Poorter et al, 2003).

Long-lived pioneer *Jacaratia spinosa* and pioneers *Urera sp.* and *Heliocarpus americanus* deviated from the trend with relatively high branch growth costs. But branch growth costs did not correlate significantly with juvenile crown exposure, when leaving these 3 species out of the test. There existed huge variation within the pioneer guild. Half of the pioneers had very low horizontal branch growth costs (*Cecropia concolor* and *Trema micrantha*), whereas the other half had high costs (*Urera sp.* and *Heliocarpus americanus*). It seems there were two different strategies within the pioneer guild with respect to branch growth economy.

The calculated branch growth costs in g dry wood per m branch were very low (median 0.2 g/m), compared with other studies (Morgan and Cannel 1988). The branch diameter for 1 m of horizontal branch was calculated in pure bending. For a branch only own weight was used, no lateral branches and no foliage were attached to the main branch. A limited end point deflection of the branch was not used either. Growth costs were only used for interspecific comparisons. An additional approach could be to compare the observed weight of the branches per unit of observed length of the branch, corrected for its angle to the horizontal.

#### 6. Do horizontal branch growth costs affect crown development? Do wood properties, safety factors and horizontal branch growth costs affect maximum adult stature?

When species have relatively high horizontal branch growth costs it is hypothesised that they grow less horizontal branches and more vertical branches; less wide crowns and deeper crowns. There is a significant negative correlation between proportion of horizontal branches and horizontal branch growth costs. Species grew less horizontal branches when they cost more (Fig. 18). Also in this correlation it seemed the trend was inflicted by the deviating species *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus*, which are also the species with the lowest wood densities. Correlation analysis without these 3 led to no significance. So, for the remaining group of species no trend could be found.

With higher branch growth costs species developed less wide crowns, valid for all species and for all species, excluding *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus* (Fig. 19). There was no significant relation between crown height and crown slenderness.

Investing energy in height growth rather than lateral crown growth allows a rapid vertical stem extension, but crown diameter has to be sufficiently small to reduce the risk of mechanical failure (Poorter *et al.* 2003). Also, with increasing tree height crowns had a greater relative crown depth (Sterck and Bongers 2001). Species of short adult stature had wider crowns than species of tall adult stature (Sterck and Bongers 1998). Limited carbon budgets of shade trees may limit their crown extension, horizontally and vertically (Sterck *et al.* 2001). A study with saplings of six Bolivian rain forest tree species showed that species differed largely in realised height and crown expansion per unit support biomass, but this could not be related to differences in their shade-tolerance (Poorter and Werger 1999).

The relation between maximum adult stature and wood strength and the direction of this relation are difficult to predict. An increase in wood strength could result in a higher maximum adult stature from a mechanical point of view. But from an ecological point of view short adult stature species need a higher wood strength and density to survive the dangers of the understorey (falling branches, fungal infection). However, an increase in strength is very often accompanied by an increase in density. This could counterbalance the positive effect of strength on maximum adult stature, resulting in a higher own weight to support. Maximum adult stature was not significantly correlated to wood density, strength, safety factor or branch growth costs, when all species were pooled (Fig. 20; Table 6).

When the same correlations were tested for 2 separate groups (shade-tolerant versus pioneer-group) remarkable, opposed correlations were found (not all correlations were significant; Fig. 21; Table 7). For the shade group the trend seemed that wood density, strength and safety factor decreased with an increase of maximum adult stature. The pioneer group showed the exact opposite: wood density, strength and safety factor increased with an increase of maximum adult stature. For the shade group horizontal branch growth costs increased with an increase of

maximum adult stature. Whereas, for the light group horizontal branch growth costs decreased with an increase of maximum adult stature. The bending safety factor did not show opposite correlation coefficients, but these coefficients were not significant.

A study of Falster and Westoby (2005) showed comparable opposed correlations for potential tree height with wood density for species in a successional set and species in a light gradient set. The successional set of Falster and Westoby (2005) could be matched with the shade-tolerant and partial shade tolerant species in this study (shade group). The light gradient set matched the long-lived pioneer and pioneer species (pioneer group). These opposed correlations found by Falster and Westoby (2005) supports the idea of 2 distinct trait-mediated axes of coexistence among short and tall plant species within vegetation. Also in general, light demand and adult stature represent independent axes of architectural differentiation, affecting tree architecture in different ways, thus contributing to the coexistence of rain forest tree species (Poorter *et al.* 2003; in press). The pioneer group deals with a successional gradient. These pioneer species establish in an early phase of succession. Light demand requires rapid height growth with low construction costs to reach or maintain in the canopy, whereas larger adult stature species need to grow to reach their reproductive size (Poorter *et al.* 2003). The shade-tolerant group of species all establish in a later phase of succession and partition the vertical light gradient in the forest.

## Conclusions

For this set of rain forest tree species wood density was a very good predictor for wood strength and stiffness. With increasing density the strength increased, as did the stiffness. Horizontal branches had a higher dry wood density than vertical stems, but horizontal branches had a lower green and saturated density than vertical stems. This could be explained by vertical stems being relatively more important for transportation of water and nutrients. Therefore, vertical stems have more and/or larger vessels than horizontal branches. Wood density and strength decreased along the successional gradient going from shade-tolerant to pioneer species.

The buckling- and bending safety factors differed significantly between species, but between guilds safety factors did not differ. The buckling safety factor differed almost significantly between guilds. The trend seemed a decrease in buckling safety factor going from shade-tolerant to pioneer. A pioneer with a rapid height growth seemed to have a lower safety factor to cut down height extension costs. Shade-tolerants seemed to have a higher safety factor for survival advantages, reducing the risk of damage from falling debris and fungal infection. No trend was discovered for the bending safety factor. It could be that, compared to shade-tolerants, pioneers maintain a similar level of safety, but minimising bending loads with different branching patterns, *e.g.* more upward orientation, less lateral branches or laterals positioned closer to the base of the main branch.

Horizontal branch growth costs differed significantly between species, not between guilds. Within the pioneer guild two different strategies for branch growth economy were found. Half of the pioneer guild grew horizontal branches at low costs, the other half at high costs. An increasing average juvenile crown exposure was correlated to branch growth costs ( $P=0.05$ ). Species experiencing higher light levels (pioneers) seemed to have higher costs for horizontal branch growth than species in lower light (shade-tolerants). Having higher branch growth costs resulted in less horizontal branches, but this trend was mainly caused by 3 deviating species, *i.e.* *Jacaratia spinosa*, *Urera sp.* and *Heliocarpus americanus*. Horizontal branch growth costs were negatively correlated with crown width. This trend was found with and without the 3 species mentioned above. High costs led to less wider crowns. It seemed that species specialised in rapid vertical stem extension at the cost of lateral crown growth.

The maximum adult stature could not be correlated to wood density, strength or safety factors, when all species were pooled. However, subdividing the species in 2 groups, (partial) shade-tolerant vs. (long-lived) pioneer group resulted in opposing correlations. For the shade group the trend was that wood density, strength and safety factor decreased, when maximum adult stature increased. The pioneer group showed the exact opposite: wood density, strength and safety factor

increased, when maximum adult stature increased. Light demand requires rapid height growth with low construction costs to reach or maintain in the canopy, whereas larger adult stature species need to grow to reach their reproductive size. Light demand and adult stature represent 2 independent axes of differentiation, influencing the architecture and crown development of a tree.

Recommendations for future research are enlarging the guild of pioneer species to investigate the 2 distinct strategies regarding high versus low horizontal branch growth costs more profoundly. Whether a subset of 30 species is sufficient to extrapolate for the whole tree species community of over 150 species could be questioned. However, the set used in this study covered a large range for wood density and strength. Expanding the number of species is especially valuable for long-lived pioneers and pioneers, since they were relatively poorer represented in the set. It could be interesting to investigate whether differences in light response do occur for older-aged trees. In this set of young, sapling trees no differences between dark- and light-grown individuals were found. Maybe for older trees these differences do develop. An analysis on the strength of horizontal branches versus vertical stems could be interesting besides the density differences found. Different patterns in horizontal-vertical strength for guilds or species could exist, influencing crown development and tree architecture. Furthermore, it would be a challenge to come to mechanical models that incorporate the dynamic loads together with the static loads, giving a better representation of real loads on trees. Finally, the calculated growth costs were rather low; a comparison with the actual weight invested per branch length could be valuable.

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## Appendix

### Summary table species – wood properties

Summary table with species common name and code; scientific name and family; guild (1=shade-tolerant; 2=partial shade-tolerant; 3=long-lived pioneer; 4=pioneer); CE5 the average juvenile crown exposure at 5m (Poorter *et al.* in press), CPI-values after Dawkins and Field 1978; average maximum adult stature (Poorter *et al.* in press); average tree height H; average crown diameter D; average crown height H; average diameter at breast height DBH; green, dry and saturated density for horizontal branch-, vertical stem-parts and mean; strength in bending (Modulus of Rupture) and in compression; stiffness or flexibility (Young's Modulus of Elasticity).

Species common name	Species scientific	Family	Traits			Tree morphology				Density									Strength		
			guild	max adult CE5	stature	Tree H	Crown H	Crown D	DBH	green			saturated			dry			Modulus of Rupture	Compress-ion strength	Modulus of Elasticity
			-	-	-	cm	cm	cm	mm	Hor	Ver	mean	Hor	Ver	mean	Hor	Ver	mean			
Ajo-ajo	<i>Galesia integrifolia</i>	Phytolaccaceae	3	1.87	31.7	270	184	142	14.9	0.95	0.95	0.95	1.02	0.96	0.98	0.39	0.35	0.37	48.93	17.99	5789
Aliso	<i>Stylogyne ambigua</i>	Myrsinaceae	1	1.50	10.1	263	159	148	17.5	1.07	1.14	1.12	1.09	1.16	1.14	0.42	0.43	0.42	56.83	20.33	5291
Ambaibo negro	<i>Cecropia concolor</i>	Cecropiaceae	4	2.84	22.2	304	58	111	17.3	-	0.75	0.75	-	0.81	0.79	-	0.15	0.17	25.23	10.26	4705
Arrayan hoja chica	-	Myrthaceae	1	1.50	7.1	271	124	153	16.1	1.05	1.10	1.09	1.14	1.13	1.13	0.52	0.56	0.54	66.22	21.07	5383
Baboso	<i>Heliocarpus americanus</i>	Tiliaceae	4	2.82	21.1	307	169	132	20.8	0.73	0.71	0.72	0.83	0.78	0.80	0.18	0.20	0.18	13.79	5.37	2386
Blanquillo	<i>Ampelocera ruizii</i>	Ulmaceae	1	1.65	29.9	277	164	158	14.1	0.97	1.02	1.00	1.05	1.07	1.06	0.48	0.53	0.50	63.98	24.30	6252
Chocolatillo	<i>Erythrochiton fallax</i>	Rutaceae	1	1.48	5.1	271	235	125	20.7	0.97	1.03	1.01	1.07	1.08	1.08	0.42	0.45	0.44	45.61	17.81	2302
Conservilla	<i>Alibertia verrucosa</i>	Rubiaceae	1	1.71	12.2	254	185	158	14.7	0.96	1.10	1.05	0.99	1.16	1.11	0.53	0.56	0.54	76.82	28.41	6682
Coquino	<i>Pouteria nemorosa</i>	Sapotaceae	2	1.56	33.8	331	164	170	19.6	1.03	1.04	1.04	1.10	1.09	1.06	0.46	0.44	0.45	53.62	18.41	5265
Gabetillo amarillo	<i>Aspidosperma rigidum</i>	Apocynaceae	2	1.91	27.0	315	180	148	17.1	1.05	1.04	1.04	1.16	1.07	1.10	0.51	0.46	0.48	59.79	23.53	4875
Gargatea	<i>Jacaratia spinosa</i>	Caricaceae	3	2.74	21.6	320	95	100	25.6	0.91	0.95	0.95	0.88	0.95	0.85	0.12	0.11	0.08	7.59	3.50	898
Huevo de perro	<i>Peschiera australis</i>	Apocynaceae	1	1.79	16.3	270	173	159	19.0	1.03	1.01	1.02	1.05	1.05	1.05	0.37	0.34	0.35	44.86	18.22	3475
Jichituriqui colorado	<i>Aspidosperma cylindrocarpon</i>	Apocynaceae	2	1.85	30.3	293	214	157	16.6	1.07	1.05	1.06	1.09	1.07	1.08	0.47	0.43	0.45	60.11	26.27	4242
Laurel	<i>Ocotea sp.</i>	Nyctaginaceae	2	1.40	26.3	264	132	163	17.7	0.91	0.96	0.94	0.97	1.00	0.99	0.34	0.32	0.33	51.67	18.31	5179
Leche-leche	<i>Sapium glandulosum</i>	Euphorbiaceae	3	2.00	29.1	302	181	144	20.5	0.86	0.88	0.87	0.87	0.92	0.91	0.29	0.27	0.28	35.14	15.23	4494
Lúcuma	<i>Pouteria macrophylla</i>	Sapotaceae	2	1.68	26.6	296	133	147	17.0	1.07	1.07	1.07	1.09	1.10	1.09	0.43	0.41	0.42	43.40	16.95	4171
Maní	<i>Sweetia fruticosa</i>	Fabaceae	3	1.75	29.8	300	143	209	17.3	1.07	1.07	1.07	1.14	1.12	1.12	0.56	0.54	0.55	87.63	29.20	7765
Negrillo hoja plateada	<i>Ocotea guianensis</i>	Lauraceae	3	1.86	24.4	333	160	195	20.5	0.85	0.86	0.86	0.91	0.86	0.88	0.42	0.40	0.41	56.26	20.78	6322
Negrillo tropero	<i>Licaria triandra</i>	Lauraceae	1	1.75	11.0	253	150	176	15.4	1.02	1.02	1.02	1.04	1.04	1.04	0.49	0.47	0.48	61.35	21.66	5938
Ochoó	<i>Hura crepitans</i>	Euphorbiaceae	2	2.00	41.2	284	113	130	19.0	0.78	0.79	0.78	0.84	0.84	0.84	0.24	0.25	0.25	26.94	11.63	3588
Ojoso colorado	<i>Pseudolmedia laevis</i>	Moraceae	1	1.46	34.3	269	173	141	16.6	1.01	1.05	1.04	1.04	1.11	1.09	0.48	0.45	0.46	50.73	18.18	4039
Pica-pica	<i>Urera sp.</i>	Urticaceae	4	2.60	12.7	302	101	121	20.2	0.92	0.93	0.93	0.94	0.94	0.88	0.16	0.18	0.13	16.22	3.36	2614
Sama colorada	<i>Cupania cinerea</i>	Sapindaceae	2	2.07	21.9	303	142	109	14.0	1.02	1.07	1.05	1.08	1.10	1.09	0.50	0.50	0.50	64.35	24.08	7578
Sapaymo colorado	<i>Hirtella triandra</i>	Chrysobalanaceae	1	1.37	11.3	288	218	193	16.3	1.10	1.10	1.10	1.15	1.10	1.12	0.58	0.54	0.56	80.28	24.76	7248
Sawinto falso	<i>Eugenia florida</i>	Myrthaceae	1	1.73	7.7	272	170	151	15.4	1.08	1.14	1.12	1.15	1.20	1.19	0.56	0.54	0.55	68.00	23.81	7454
Sawinto propio	<i>Myrcianthes sp.</i>	Myrthaceae	2	1.50	25.2	299	191	189	19.4	1.09	1.10	1.09	1.12	1.14	1.13	0.58	0.53	0.56	79.07	29.92	6318
Tarara amarilla	<i>Centrolobium microchaete</i>	Fabaceae	3	2.45	25.6	301	140	145	17.5	0.80	0.82	0.81	0.87	0.89	0.89	0.34	0.33	0.33	42.54	15.97	5694
Trompillo	<i>Guarea guidonia</i>	Meliaceae	1	1.81	8.9	296	169	133	18.5	0.99	1.02	1.01	1.11	1.05	1.07	0.36	0.41	0.39	50.92	19.84	5119
Uvilla	<i>Trema micrantha</i>	Ulmaceae	4	3.62	31.3	325	169	169	19.6	0.65	0.68	0.67	0.75	0.75	0.75	0.23	0.20	0.21	25.09	11.42	3533
Verdolago	<i>Terminalia oblonga</i>	Combretaceae	2	2.06	33.0	260	153	137	15.5	0.91	0.94	0.93	0.96	0.99	0.98	0.40	0.37	0.39	42.18	15.48	3996

- There was no scientific name available yet for Arrayan hoja chica